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     'Smith (1969: 36, fig. 16) described …'
     'As described (Smith 1969*a*, 1969*b*; Jones 1971)'
     'As described (Haughton & Broom 1927) …'
     'As described (Haughton *et al.* 1927) …'

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     FISCHER, P. H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* **74**: 627–634.

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     KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* **17** (4): 1–51.

     THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungreise im westlichen und zentralen Süd Afrika ausgeführt in den Jahren 1903–1905* **4** (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* **16**: 269–270.

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ANNALS OF THE SOUTH AFRICAN MUSEUM

ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

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OSTEOLOGY OF THE EARLY ARCHOSAURIAN REPTILE *ERYTHROSUCHUS AFRICANUS* BROOM

by

DAVID JOHN GOWER

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The Annals of the South African Museum publishes original research articles, revisions and review articles in natural history (palaeontology, geology, entomology, herpetology, ornithology, mammalogy, and marine and freshwater biology), social history (anthropology, archaeology and history), and art.

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OSTEOLOGY OF THE EARLY ARCHOSAURIAN REPTILE *ERYTHROSUCHUS AFRICANUS* BROOM

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(With 37 figures and 2 tables)

[*MS submitted May 1996*]
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ABSTRACT

Erythrosuchus africanus Broom (Archosauria, Erythrosuchidae) is an early, non-crown-group archosaurian reptile known exclusively from the Lower–Middle Triassic *Cynognathus* Assemblage Zone of the South African Karoo Basin. A detailed redescription of the osteology, excluding that of the braincase and tarsus, is presented, based on examination of nearly all known material. Several skull and mandibular elements are described for the first time. Aspects of the interpreted and documented osteology of particular interest include the presence of three-headed pectoral ribs, an antorbital fossa, osteoderms, and possibly pneumatized neural arches. Palatal teeth are documented in the Russian erythrosuchid *Garjainia prima*. New skeletal reconstructions of *E. africanus* are presented. Many skull elements have joint surfaces that form potentially movable articulations with other elements, but consideration of the adult cranium and mandible as whole units shows that they were not kinetic to any notable extent. The main variations in morphology among known specimens of *E. africanus* are summarized. Convincing intrinsic evidence for the recognition of more than a single species of *Erythrosuchus* is lacking. Among erythrosuchids, the distribution of apparently derived osteological features supports evidence from braincase osteology that has been interpreted as indicating that *E. africanus* and the Chinese *Shansisuchus* are more closely related to one another than either taxon is to *Garjainia prima*, although a new explicit analysis of phylogeny has yet to be performed.

Ann. S. Afr. Mus. **110** (1), 2003: 1–88, 37 figs, 2 tables, appendix.

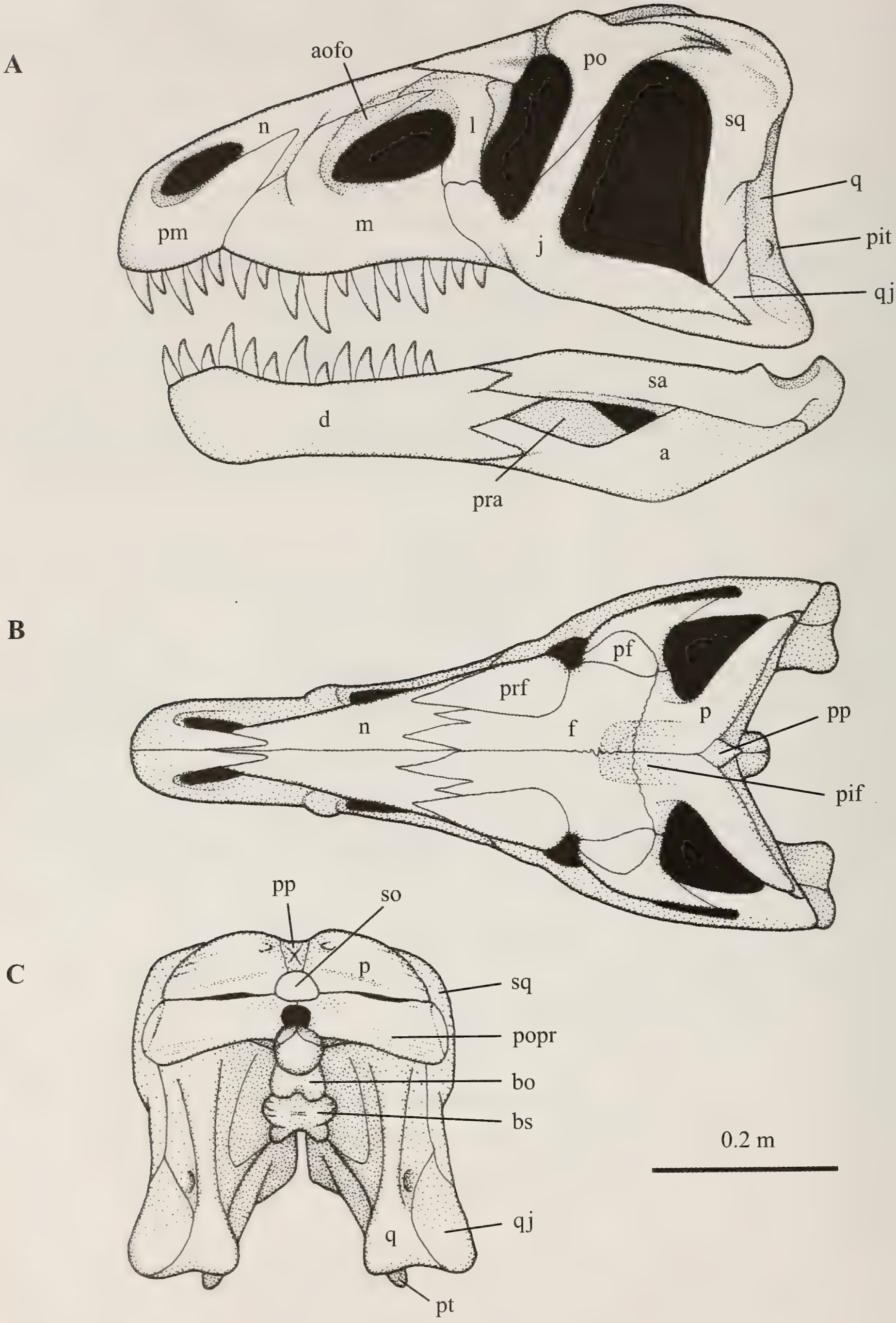

Figure 1

Erythrosuchus africanus. Restoration of skull and mandible, based largely on BPI 5207. Text should be consulted for information on variation among specimens. A. Left lateral view. B. Dorsal view. C. Occipital view.

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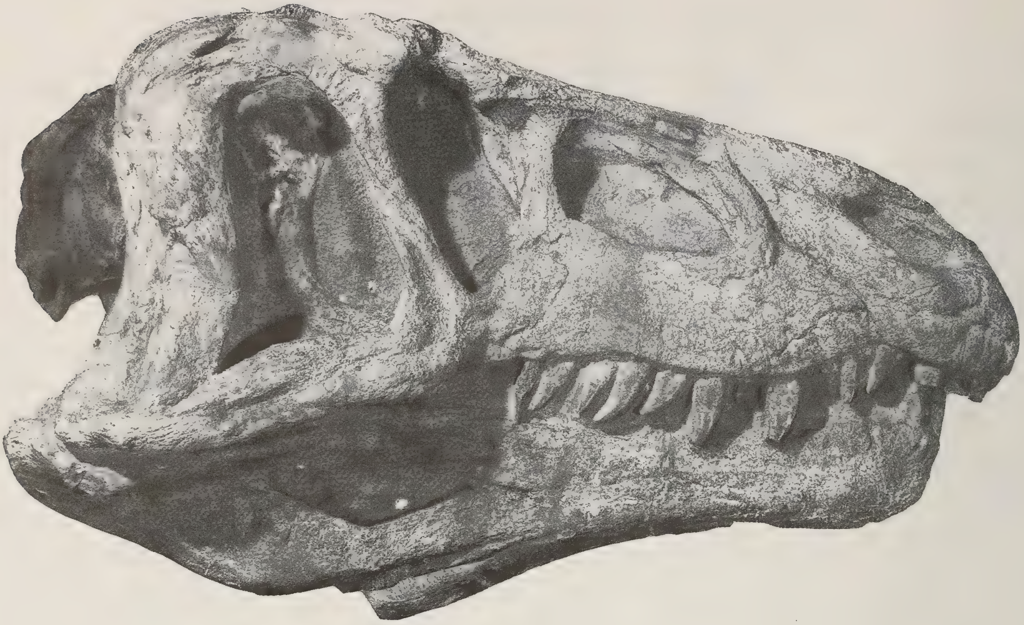

Figure 2A

Erythrosuchus africanus. Skull and mandible of BPI 5207. Right lateral view.

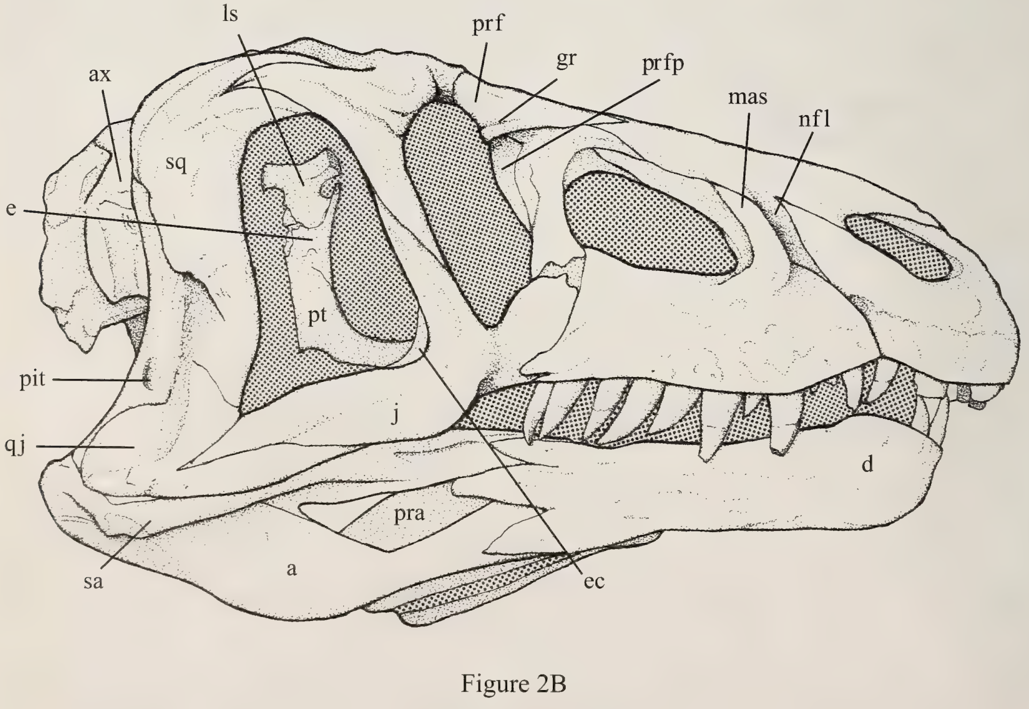

Figure 2B

Erythrosuchus africanus. Skull and mandible of BPI 5207. Right lateral view.

INTRODUCTION

GENERAL COMMENTS

Archosauria is a major clade of diapsids that consists of birds, crocodilians, dinosaurs, pterosaurs and their nearest fossil relatives. Archosaurs dominated every terrestrial and aerial large vertebrate niche for most of the Mesozoic. Recent interest in the pattern of their radiation has focused upon the application of a cladistic methodology in the inference of phylogenetic relationships, resulting in a number of major recent publications (Gauthier 1986; Benton & Clark 1988; Sereno & Arcucci 1990; Sereno 1991; Parrish 1993; Juul 1994; Bennett 1996; Benton 1999).

Whereas these studies contain a certain amount of agreement on the interrelationships of some of the main archosaurian groups (Gower & Wilkinson 1996), they are to some extent based on differing approaches to the use of the same morphological information available from the existing descriptive literature. Over the last decade the research effort directed toward reassessing basal archosaur morphology and producing detailed osteological descriptions pales in comparison with work conducted within the phylogenetic research programme. This is also evident in the fact that the cladistic analyses of archosaur relationships have focused thus far largely on the broader question of the relationships between, rather than within, the major groups—their monophyly largely being accepted *a priori*.

It could be argued that no detailed, complete osteological descriptions of any early archosaur currently exist. Indeed, since Charig & Reig (1970: 140) reported that 'the only well known [early archosaur] genera are *Chasmatosaurus*, *Erythrosuchus* and *Shansisuchus*, and even of those our knowledge is far from complete', there has been only a single and relatively brief reassessment (Cruickshank 1972) of the osteology of any adequately represented early archosaur. Despite this, the existing descriptions remain the major source of information used in the large number of recent cladistic analyses of basal archosaurs. It is the aim of this paper to make a step towards redressing the morphology–phylogenetics imbalance, by presenting a detailed revision of the osteology of *Erythrosuchus africanus*.

The taxon Archosauria is used throughout in its traditional concept (see Juul 1994). The restricted members of the Archosauria of Gauthier (1986; = Avesuchia Benton, 1999) are referred to as 'crown-group archosaurs' (= avesuchians of Benton 1999).

ERYTHROSUCHUS AFRICANUS

Erythrosuchus africanus was named and preliminarily diagnosed by Broom in 1905 on the basis of a single, incomplete post-cranial specimen (SAM–905). This was followed by a fuller description of the holotype in which Broom (1906) also referred *E. africanus* to the Phytosauria. A much more complete specimen, BMNH R3592, was the focus of a more detailed monograph by Huene (1911), who considered *E. africanus* to be a representative of a new reptilian order, the Pelycosimia, closely allied to the Pelycosauria.

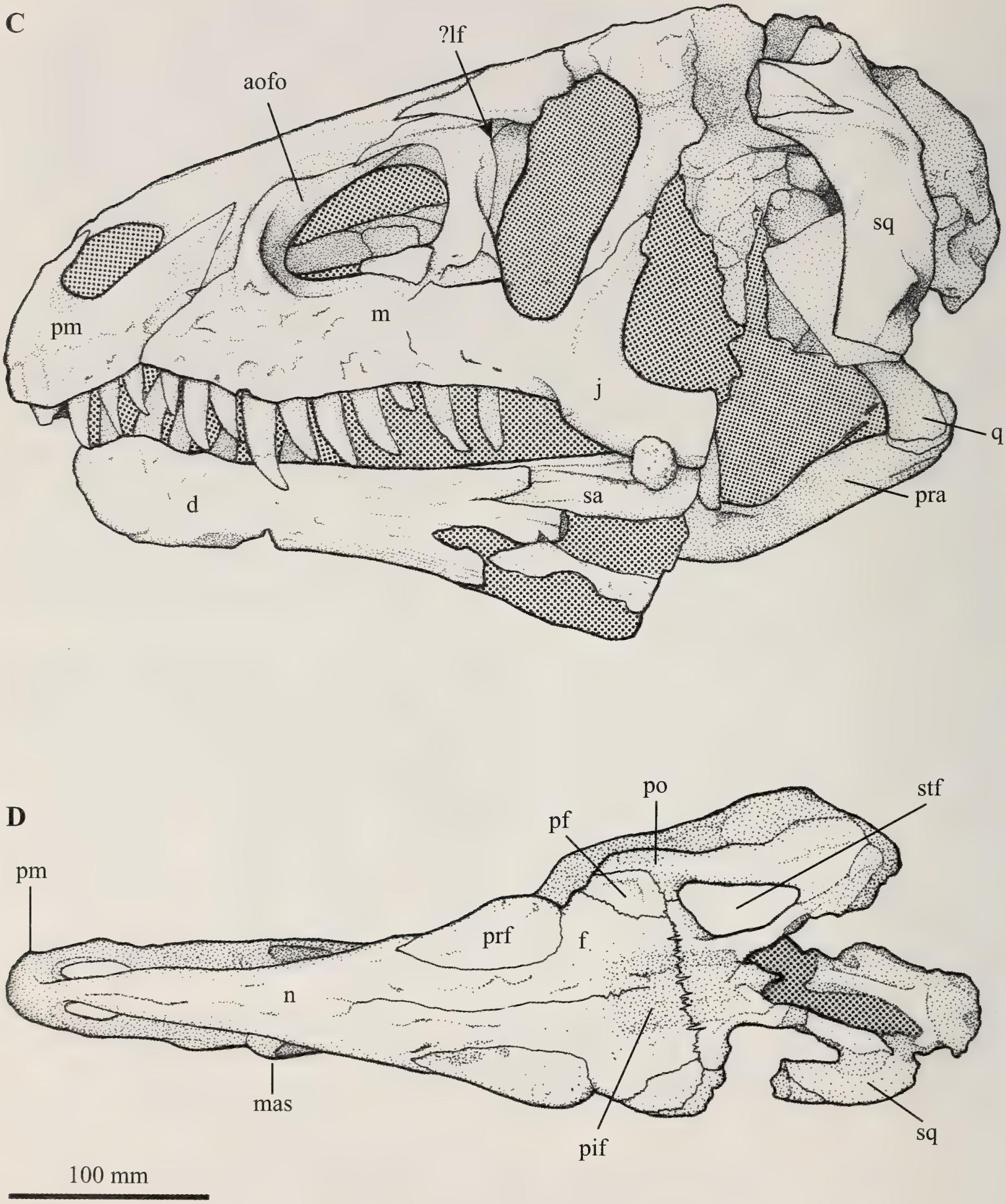

Figure 2C & D

Erythrosuchus africanus. Skull and mandible of BPI 5207. C. Left lateral view. D. Dorsal view.

Huene recognized that some material referred by Seeley (1894) to *Euskelosaurus brownii*, actually belonged to *E. africanus*. Some of the cranial material of BMNH R3592 is incomplete or missing, whereas some of the preserved elements were ignored or misidentified by Huene (e.g. laterosphenoids and palatine respectively). The informativeness of parts of Huene's description are perhaps further clouded by his belief that *Erythrosuchus* has affinities with the Pelycosauria.

Watson (1917) placed *E. africanus* in his newly erected family, Erythrosuchidae. Later systematic studies have consistently placed *Erythrosuchus* within the Archosauria in the order Thecodontia and the suborder Proterosuchia (e.g. Charig & Sues 1976). These last two taxa are commonly considered to be paraphyletic grades, and the results of cladistic analyses have placed a monophyletic Erythrosuchidae outside the archosaur crown group (e.g. Benton & Clark 1988; Sereno & Arcucci 1990; Sereno 1991; Parrish 1992, 1993; Bennett 1996; Gower & Sennikov 1997).

Further descriptive accounts of *Erythrosuchus africanus*, and particularly of the tarsus and braincase, have been presented by Huene (1920), Hughes (1963), Cruickshank (1978), Gower & Sennikov (1996*a*) and Gower (1996, 1997). Parrish (1992, fig. 6) presented a drawing of the skull of BPI 5207, but many of the sutural patterns depicted are at variance with the observations made during the current study (compare with Figures 1–2 here). There have been no substantial reassessments of most of the osteology of this important taxon since the work of Broom and Huene.

The aim of this study is to revise and correct descriptions that exist for those parts of the skeleton previously studied but not described in detail, and to cover in detail the numerous parts never previously described—in particular much of the skull and mandible. As a result of the rarity of detailed descriptions and sub-familial phylogenetic analyses of early archosaurs, it is not possible in most cases to fully assess the distribution of the features described here. Where possible, considerations of the distribution of features are given by means of comparative data.

Description of the problematic tarsal material, of a cast of the endocranial cavity, and of the detailed structure of the braincase is presented elsewhere (Gower 1996; Gower & Sennikov 1996*a*; Gower 1997).

GEOLOGICAL SETTING

The Karoo basin of southern Africa is well known for its extensive complex of mudstones and sandstones, deposited from the Permo-Carboniferous to the early Jurassic (300–190 Ma). Much of the impressive diversity of Mesozoic vertebrate remains to have been documented are known from the fluvio-lacustrine succession of sediments of the Beaufort Group (late Permian to early Triassic) of South Africa. The upper part of the Beaufort Group is represented by the *Cynognathus* Assemblage Zone, and it is from this zone that perhaps all specimens of *Erythrosuchus africanus* have been collected. The only potential exceptions would seem to be erythrosuchid specimens from the equivalently-aged Omingonde Formation of Namibia (Pickford 1995).

The *Cynognathus* Assemblage Zone has previously been equated with the upper part

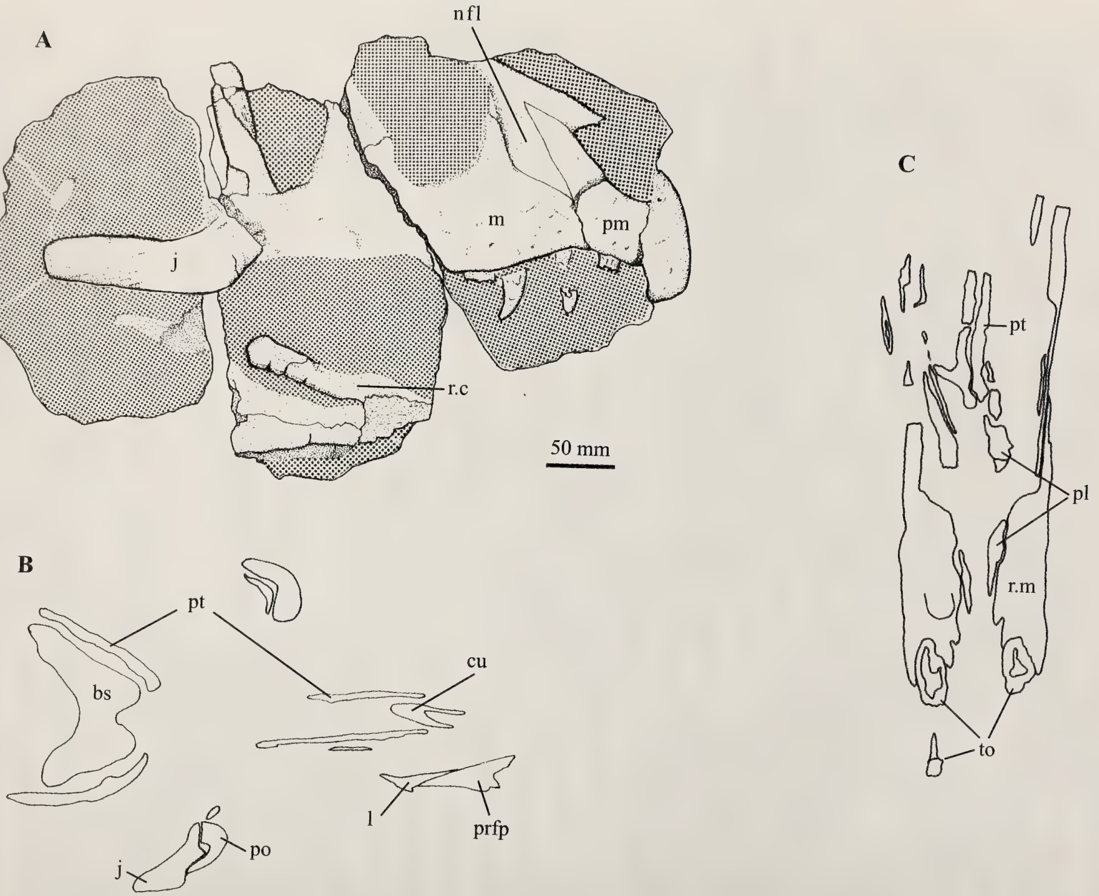

Figure 3A, B & C

Erythrosuchus africanus. Unprepared skull and mandible of BPI 3893. A. Right lateral view of three blocks with fourth, posterodorsal, block and most of mandible omitted. B. Dorsal view of posterior block. C. Posterior view of anterior block.

of the Lower Triassic (e.g. Charig & Sues 1976; Anderson & Cruickshank 1978; Sun 1980), but the most recent studies (e.g. Ochev & Shishkin 1988; Shubin & Sues 1991; Shishkin & Welman 1994; Shishkin & Ochev 1995) suggest that its vertebrate fauna is instead consistent with a lowermost Middle Triassic age. Sediments assigned to the *Cynognathus* Assemblage Zone in South Africa are best exposed in the south-western Free State and northern part of the extreme Eastern Cape Province (Kitching 1977). Recently, Welman *et al.* (1991) have also discovered vertebrate-bearing *Cynognathus* Assemblage Zone deposits in the north-eastern Free State. *Erythrosuchus africanus* specimens have been collected from a number of the best-known localities (Kitching 1977). The holotype originates from Oorlogsfontein, Aliwal North, whereas the other most important specimens were discovered in localities near Burgersdorp (BMNH R3592, BPI 2096—Geluk; NM QS1473—Winaarsbaken) or Rouxville (BPI 4680, 5207—Betjeskraal; BPI 3893—Lemoenfontein), all in the Free State. The seven specimens listed above form the basis for the majority of current knowledge of the morphology of *Erythrosuchus africanus*. Many of the approximately 60 known specimens (see Appendix I) consist of disarticulated, isolated and/or poorly preserved finds.

The *Cynognathus* Assemblage Zone vertebrate fauna contains many synapsids (e.g. *Cynognathus*, *Diademodon*, *Trirachodon*, *Bauria*, *Kannemeyeria*), at least two archosaurs (*Erythrosuchus*, *Euparkeria*), rhynchosaurs (*Howesia*, *Mesosuchus*), fish, and capitosaurid amphibians (Kitching 1977; Welman *et al.* 1991). There is generally a lack of detailed records of the preservation of individual specimens of *Erythrosuchus africanus* that might be taphonomically informative. However, a photograph of BMNH R3592 prior to preparation, shows that this incomplete specimen (missing several elements including some from the skull, the left forelimb, right forelimb epipodials, scapulae, intercentra) is disarticulated apart from the caudal vertebrae and firmly sutured elements of the skull roof and part of the braincase. The preserved elements form a concentrated jumble of bones in a flat and tightly-packed ‘conglomerate’, approximately 1.5 × 1 × 0.15 m in size. This assemblage is perhaps indicative of fluvial winnowing, and is therefore consistent with the interpretation of detailed studies of Karoo vertebrate taphonomy (e.g. Smith 1993), that the fossiliferous deposits are channel/overbank and adjacent flood plain in their origin.

MATERIALS AND METHODS

A full list of *Erythrosuchus africanus* material is presented in Appendix I. A small amount of mechanical preparation (vibrotool) was undertaken on BPI 4526. Some specimens, but most notably BPI 3893, will possibly yield new information (e.g. on the palate) when they are fully prepared. Most of the observation of specimens for this study took place in the early 1990s. Further preparation and/or collection of material may have taken place since then.

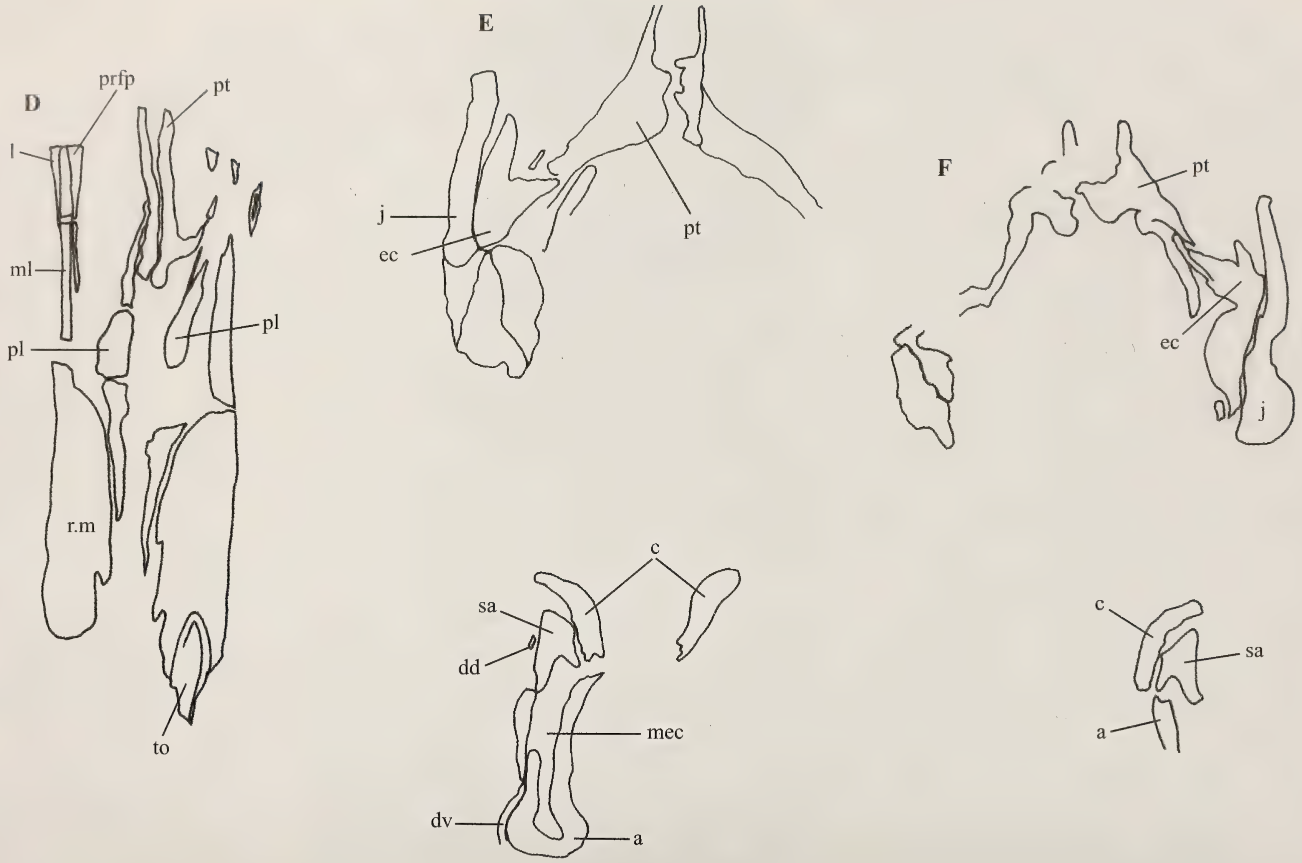

Figure 3D, E & F

Erythrosuchus africanus. Unprepared skull and mandible of BPI 3893. D. Anterior view of central block. E. Posterior view of central block. F. Anterior view of posterior block. Sections are not to same scale.

SYSTEMATICS

DIAPSIDA Osborn, 1903
ARCHOSAUROMORPHA Huene, 1946
ARCHOSAURIA Cope, 1869
Family **Erythrosuchidae** Watson, 1917
Genus *Erythrosuchus* Broom, 1905
Erythrosuchus africanus Broom, 1905

1889	Theriodont: Lydekker, pp. 572–573, pl. 54.
1890	Genus non det.: Lydekker, pp. 96–98.
1894	*Euskelosaurus brownii* Huxley: Seeley, pp. 335–340, figs 6–7.
1905	*Erythrosuchus africanus* Broom, pp. 336–337.
1906	*Erythrosuchus africanus* Broom: Broom, pp. 187–195, pl. 4.
1911	*Erythrosuchus africanus* Broom: Huene, pp. 3–25, pls 1–11.
1915	*Erythrosuchus africanus* Broom: Broom, p. 160.
1915	*Erythrosuchus africanus* Broom: Huene, p. 495, fig. 16.
1920	*Erythrosuchus africanus* Broom: Huene, p. 489, fig. 51.
1926	*Erythrosuchus africanus* Broom: Huene, pp. 44–45, figs 6–7.
1955	*Erythrosuchus africanus* Broom: Brink, pp. 146–148, fig. 2.
1963	*Erythrosuchus* Broom: Hughes, pp. 227–230, figs 1–2, 4–6.
1970	*Erythrosuchus africanus* Broom: Charig & Reig, pp. 134, 156–160, fig. 3.
1975	*Erythrosuchus africanus* Broom: Ochev, p. 102.
1976	*Erythrosuchus africanus* Broom: Charig & Sues, pp. 28, 30.
1978	*Erythrosuchus africanus* Broom: Cruickshank, pp. 161–176, fig. 1, pls 1–13.
1981	*Erythrosuchus* Broom: Brinkman, pp. 18–20, fig. 12A–B.
1992	*Erythrosuchus africanus* Broom: Parrish, pp. 94–101, figs 2, 6.
1994	*Erythrosuchus africanus* Broom: Juul, pp. 3–4, 6, 12.
1996	*Erythrosuchus africanus* Broom: Gower, pp. 349–358, figs 2–6.
1996*a*	*Erythrosuchus africanus* Broom: Gower & Sennikov, pp. 581–583, figs 1–2.
1996*b*	*Erythrosuchus* Broom: Gower & Sennikov, pp. 896–900, table 1.
1997	*Erythrosuchus africanus* Broom: Gower, pp. 557–573, figs 1–11.
1997	*Erythrosuchus africanus* Broom: Gower & Sennikov, table 2.
1997	*Erythrosuchus africanus* Broom: Witmer, pp. 12, 52.
2001	*Erythrosuchus africanus* Broom: Gower, pp. 120–121, fig. 2.

Diagnosis

Large erythrosuchid; skull and total snout–tail length possibly up to 1 m and 5 m respectively. Skull tall and narrow, with antorbital fenestra and fossa. Fossa surrounds antorbital fenestra. Ascending process of maxilla raised laterally and separated from posterodorsal process of premaxilla by ventral flange of nasal. Jugal excluded from antorbital fenestra by maxilla-lacrimal contact. Frontals L-shaped. Prefrontals triangular with caniculae on dorsal surface. Fossa present in pineal region. Postparietal forms

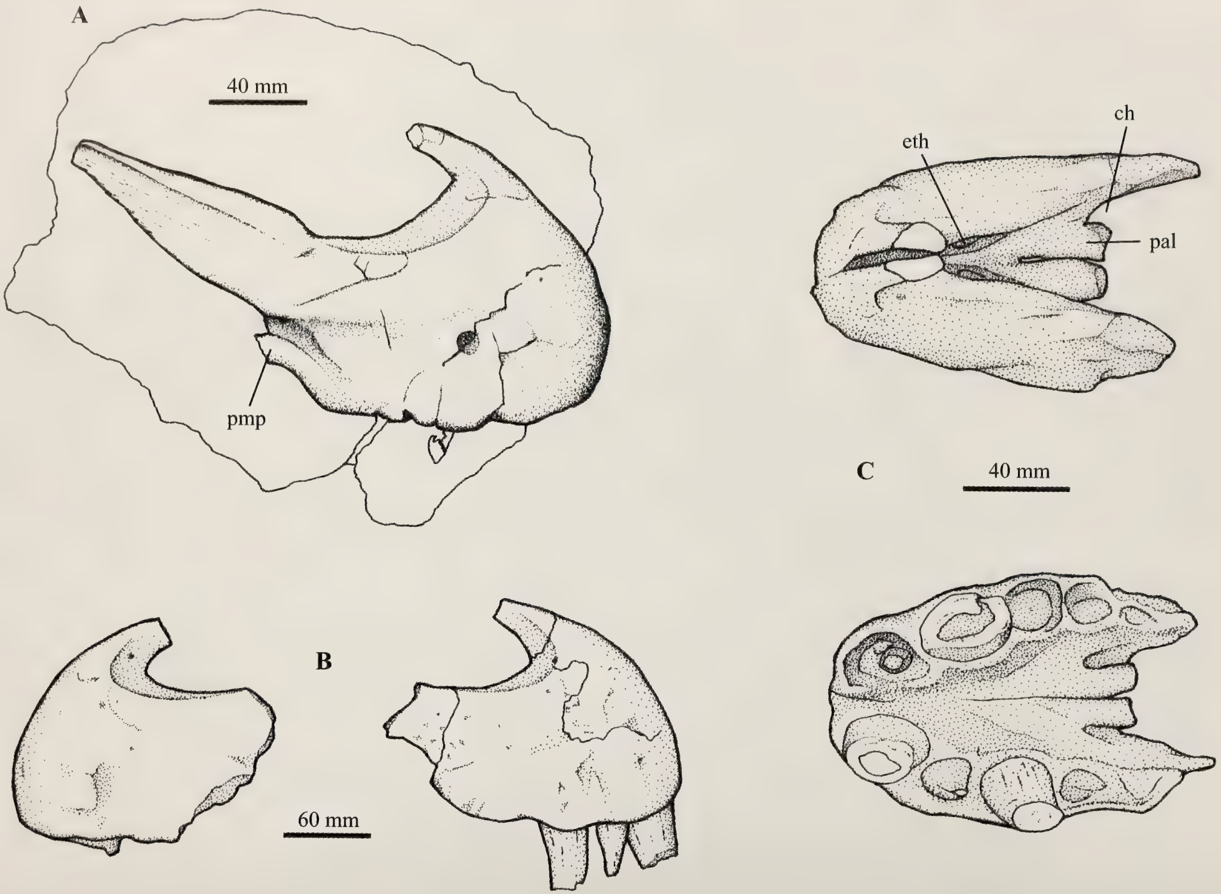

Figure 4

Erythrosuchus africanus. A. Lateral view of incompletely prepared right premaxilla, BPI 4526. B. Lateral views of premaxillae of BMNH R3592. C. Dorsal and ventral views of premaxillae of BMNH R3592.

pyramidal occipital peg. Quadratojugal very nearly or completely excluded from lateral temporal fenestra by squamosal-jugal contact. Posterior process of postorbital with incised groove. Squamosal with pleat in posterior margin of descending ramus. Foramen absent between quadrate and quadratojugal. Post-temporal fenestrae no more than narrow slits. Transverse processes of parietal with posteromedial tubercles. Palatal teeth absent on pterygoid, uncertain on palatine and vomer.

Supraoccipital excluded from foramen magnum. Basioccipital excluded from foramen magnum and floor of endocranial cavity. Basisphenoid midline exposure absent on floor of endocranial cavity. Ventral ramus of opisthotic recessed within stapedial groove. Stapedial groove with small bulge. Medial wall of otic capsule not fully ossified. Metotic foramen undivided. Lagenar region not differentiated or elongated. Basisphenoid intertuberal plate small. Laterosphenoid short and thick, with an anterodorsal channel.

Dentary expanded anteriorly and with three tapering posterior processes. Retroarticular region of jaw short, with low ridge on posterodorsal surface. Five premaxillary teeth; approximately 11 maxillary and 13 dentary teeth.

Estimated 25 presacral, two sacral, and at least 35 caudal vertebrae. All vertebrae short. Separate intercentra present (probably throughout precaudal column). Dorsal neural arches pierced by subdivided foramina, perhaps pneumatic in nature. Three-headed ribs present in pectoral region. Scapula large and coracoid relatively small. Humerus robust, with quadrangular deltopectoral crest. Femur with intertrochanteric fossa and prominent ventral trochanter positioned slightly away from proximal end. All limb bones with rugose/unfinished articular ends. Astragalus spherical. Calcaneum plate-like and with laterally directed tuber. Fourth distal tarsal with ventral peg. First two distal tarsals and centrale absent. Metatarsal III the longest. Osteoderms present.

Holotype

SAM–905 in the South African Museum, Cape Town. Incomplete postcranial skeleton from the locality of Oorlogsfontein, Kraai River, a few miles east of Aliwal North, Eastern Cape Province, South Africa—*Cynognathus* Assemblage Zone, Upper Beaufort series, Karoo system; upper part of the Lower Triassic or lower part of the Middle Triassic.

Material

A list of current material referred to *Erythrosuchus africanus* is given in Appendix I.

Remarks

Tatarinov (1961) synonymized the Russian genera *Vjushkovia*, *Garjainia*, *Dongusia*, and the Argentinian *Cuyosuchus* with *Erythrosuchus*, but maintained distinctions between respective species. These generic synonyms were rejected by Young (1964), Charig & Reig (1970) and Charig & Sues (1976) and this view is accepted here. (All except the Argentinian material has been examined.) Sennikov rejected the congeneric status of *E. africanus* and *E. magnus* Ochev, 1980, and established the genus *Uralosaurus* for the latter (Gower & Sennikov 2000). The taxonomy of *Erythrosuchus* is discussed further below.

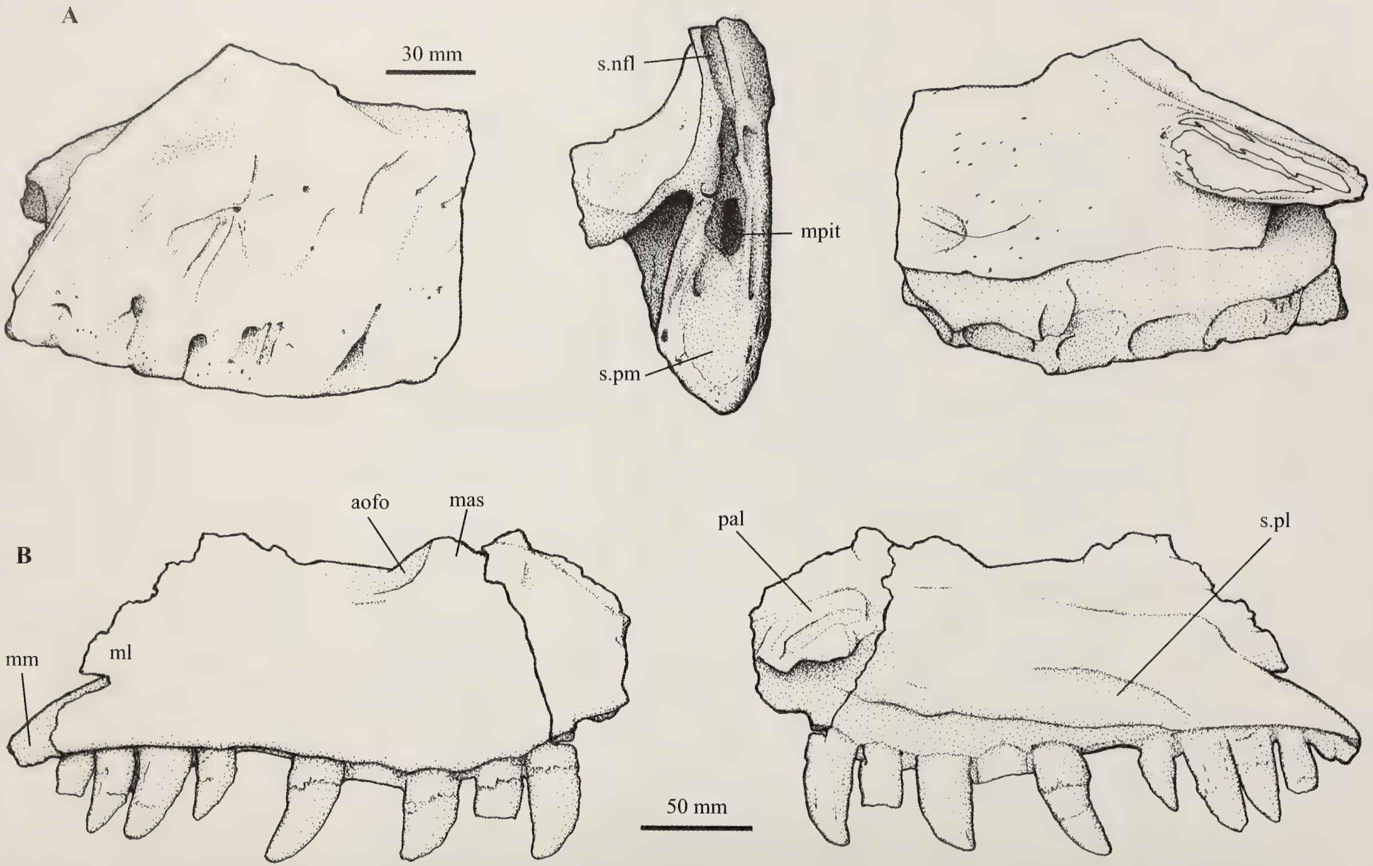

Figure 5

Erythrosuchus africanus. A. Left maxilla of SAM–K1098 in lateral, anterior and medial views. B. Right maxilla of BPI 4680 in lateral and medial views.

DESCRIPTION

SKULL (for restoration, see Fig. 1)

The skull of *Erythrosuchus africanus* bears many features common to early, presumably carnivorous, archosaurs: it is relatively tall and narrow, and possesses an antorbital fenestra and fossa and recurved, serrated teeth. Notable cranial kinesis is absent (see discussion below), and 'articulation' is used throughout to describe contact without implying that a movable joint was present between two or more articulating elements.

Dermal bones of the skull roof

The premaxilla (Figs 2–4) is a short and narrow bone with two posteriorly directed processes attaching it to the nasal and maxilla. A slender anterodorsal process extends back to articulate with a groove on the dorsal surface of the nasal. Just behind the medial edge of the base of this process is a foramen interpreted as probably transmitting the medial ethmoidal nerve. Contact with the maxilla is achieved with a long and tapering, posterodorsally directed process. The dorsal edge of this process forms the posteroventral border of the external naris, the ventral edge contacts the front of the maxilla, and the medial face of the posterior part of the process articulates with a shallow and closely matching depression on the lateral flange of the nasal. Preparation of BPI 4526 revealed the presence of a small posteriorly directed peg near the base of this process (Fig. 4A). This peg, probably eroded away in BMNH R3592 and not visible in other specimens, articulates with a pit on the anterior edge of the maxilla. A similar premaxillary peg is present in this position in *Shansisuchus kuyeheensis* (Cheng, 1980).

Medially there is a short and slender palatal process. The area of symphysis between the premaxillae covers a large anterodorsal part of their medial surface. Each premaxilla holds five teeth.

The maxilla (Figs 2, 5, 6) is a long, narrow element that bears most of the upper jaw dentition and forms the anterior and ventral border of the oval-shaped antorbital fenestra. Anteriorly it articulates with the lacrimal, nasal, and premaxilla, whereas posteriorly it firmly interlocks with the jugal and contacts the lacrimal.

The maxilla articulates with both the nasal and the anterior of the lacrimal by means of a posterodorsally directed ascending process. The anterior edge of this process is grooved to accommodate the posteroventral edge of the anterolateral flange of the nasal. The base of the ascending process is raised to form a lateral ridge. Behind this, the posteroventral edge of the process is thin and inset, and it extends posteriorly to articulate with a ventral groove on the nasal before terminating in a depression on the lateral surface of the anterior ramus of the lacrimal. As a result of this arrangement, the antorbital fenestra is countersunk within a larger lateral depression—the antorbital fossa.

The anterior margin of the maxilla bears a broad, shallow groove that articulates with the premaxilla. Situated within this groove is a posteriorly directed pit that accepts the peg on the premaxilla. This pit is clearly seen in SAM–K1098 (Fig. 5A) and in the less well-preserved maxilla of BMNH R3592. The present study disagrees with Juul's (1994: 12)

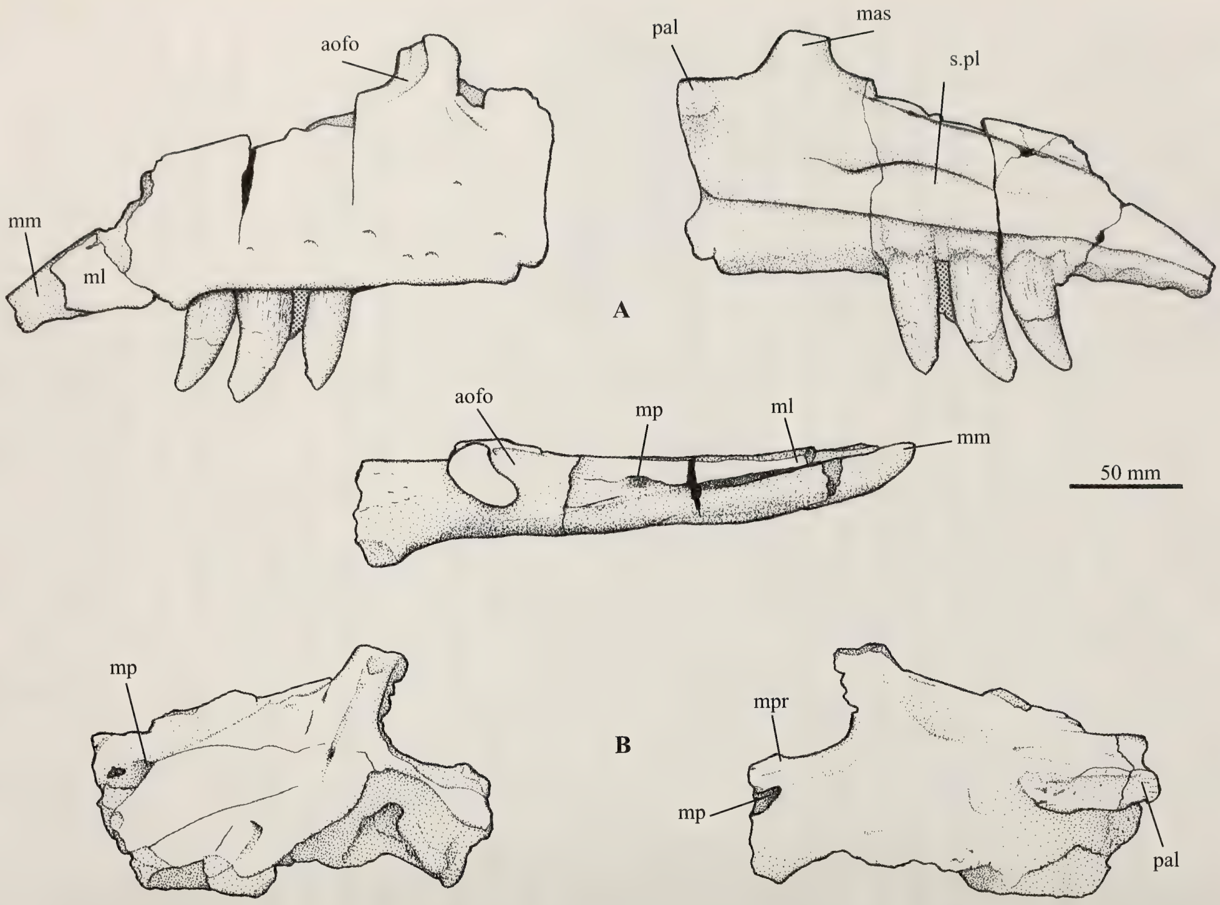

Figure 6

Erythrosuchus africanus. A. Right maxilla of BPI 2529 in lateral, medial and dorsal views. B. Left maxilla of BMNH R3592 in lateral and medial views.

identification in BPI 5207 of a 'dorsoventrally elongated fenestra between the premaxilla and maxilla', comparable to openings in this region in other erythrosuchids and some crown-group archosaurs. No fenestra could be located on the largely undisturbed right or the somewhat flattened left side of BPI 5207, and there is no evidence for the presence of an elongated fenestra in other (albeit mostly disarticulated) specimens. Openings in this region of the skulls of archosaurs come in a diversity of forms. Among those taxa discussed by Juul (1994), for example, the openings in *Shansisuchus* and *Chalishevia* are large circular fenestrae lying between premaxilla, maxilla, and nasal, with a neighbouring fossa in the latter element (Gower & Sennikov 2000). This is quite different to the similarly positioned openings in the dinosaurian and rauisuchian taxa that Juul mentioned. In addition to requiring more precise information on the form of any foramina or fenestrae in this region, the function and potential homology of these features is badly in need of reinvestigation (Gower 2000).

The ventral edge of the maxilla is sigmoidally curved in lateral view and this accentuates the wide notch between the ventral edges of the premaxilla and maxilla. The maxilla tapers posteriorly and meets the jugal. Posterodorsally, the ventral arm of the lacrimal also contacts the maxilla. Details of this articulation are not known but it definitely excludes the jugal from the border of the antorbital fenestra.

A feature observed on BMNH R3592 is the presence of an incomplete, small dorsal projection that notches the ventral border of the antorbital fenestra (Fig. 6B). This is perhaps superficially similar to the condition in *Euparkeria capensis* as reconstructed by Ewer (1965, fig. 2). The presence of this projection is also suggested by a broken surface in SAM–K1098, but it is apparently absent or not preserved in other specimens.

Medially, the palatal process is positioned far anteriorly. Posteriorly it is stout and firmly fused to the medial wall, whereas anteriorly it is much thinner dorsoventrally and slopes ventromedially to form an overhang (Fig. 5B). It is possible that the opposite palatal processes of the maxillae would not quite have made contact medially because of their narrowness. How they articulated with the premaxillae and vomers is not known.

The medial features of the posterior half of the maxilla are exposed in BPI 2529 (Fig. 6A) and 4680 (Fig. 5B). This part of the maxilla is composed of a thin dorsal and lateral part, and a thicker ventral and medial component. Posteriorly, as the maxilla tapers to a point, the thick medial and thin lateral parts become separated and the small gap between them receives the central flange of the divided anteroventral arm of the jugal to form an intimately interlocking articulation. A small posterodorsally open pit lies between the lateral and medial parts of the maxilla of BPI 4680 and 2529 (Fig. 6A), whereas the condition in BPI 4540 and BMNH R3592 is less clear. BPI 4540 seems to have a small pit, perhaps equivalent to that in BPI 2529 and 4680 but, positioned a short distance in front of this, is a much larger pit. This seems to be equivalent to a similarly placed pit in BMNH R3592, and they probably represent the posterior opening of a neurovascular canal. The absence of the larger pit in BPI 2529 and particularly 4680 could possibly be explained by poorer preservation. This feature is also seen in other archosaurs (e.g. Gower 1999) and probably has a broad distribution.

The medial surfaces of BPI 4680 and 2529 bear scars that are interpreted as the area of articulation with the palatine.

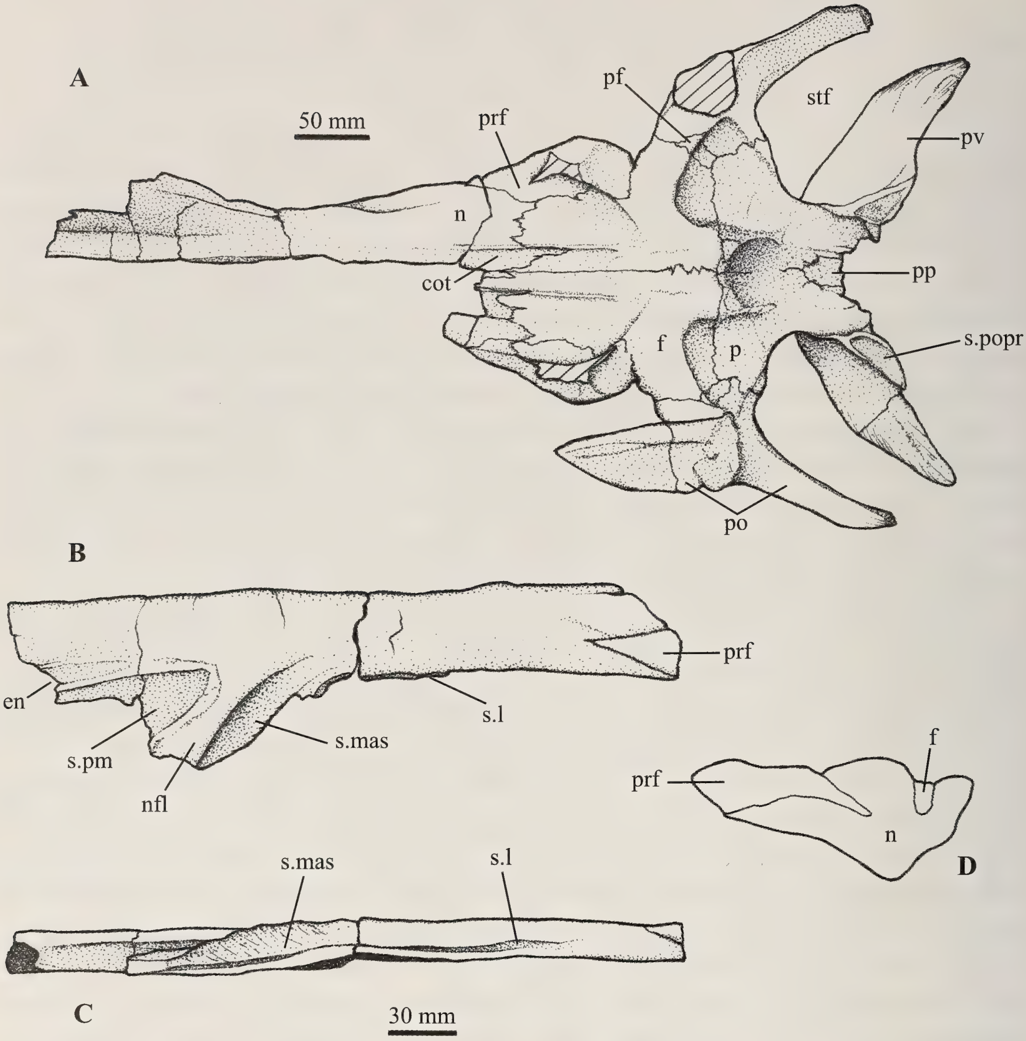

Figure 7

Erythrosuchus africanus, NM QS1473 skull roof. A. Ventral view. B. Lateral view of anterior part. C. Ventral view of anterior part. D. Posterior view of anterior part, not to same scale.

The nasal (Figs 2, 3, 7, 8) is a long and narrow bone forming much of the anterior part of the skull roof. Behind the naris, a large vertically descending flange bears a broad, shallow groove that receives the posterior process of the premaxilla. Here the nasal is at its ventral limit, and it separates the posterior process of the premaxilla from the ascending process of the maxilla (Figs 2, 3). The posteroventral edge of the vertical nasal flange articulates with the groove on the anterior edge of the ascending maxillary process. A bevelled posteroventral edge and a shallow groove at the posterior limit of the vertical nasal flange (Fig. 7B, C) articulate intimately with the rest of the tapering maxillary process. A second groove, originating a short distance behind this, receives the dorsal edge of the anterior arm of the lacrimal.

Sutural contact between the nasal and the overlapping frontal and prefrontal is achieved via long interdigitating processes (Fig. 8). A transverse section through the skull roof of NM QS1473 shows that the prefrontal is also intimately received by an invagination on the dorsal surface of the nasal (Fig. 7D). The ventral surface sutures with the prefrontal and frontal are less strongly interdigitating. The ventral surfaces of the nasals carry the anterior part of a wide channel for the olfactory tract, and an area for the nasal glands (Witmer 1997: 12).

The lacrimal (Figs 2, 3) is currently known only from BPI 5207 and 3893. Dorsally, the posterior border of the lacrimal articulates with the ventrolateral surface of the prefrontal. Anterior to this is a thickened dorsolateral ridge that articulates with the prefrontal and the posterolateral edge of the nasal. The lacrimal curves slightly downwards from this point to contact the ascending process of the maxilla. The posterior end of the maxilla rests in a groove between the inset ventral and raised dorsal levels of the stepped lateral surface of the lacrimal. This stepped area contributes to the antorbital fossa (Fig. 2).

The descending arm of the lacrimal meets, and laterally overlaps, the anterior end of the jugal. It also meets the posterodorsal corner of the maxilla but the details of the articulation are unclear, even in BPI 3893—which is sectioned in this region (Fig. 3). Most of the posterior margin of the lacrimal is excluded from the orbit by the prefrontal. A pit on the border between the left lacrimal and prefrontal of BPI 5207 (Fig. 2C) possibly indicates the posterior opening of the nasolacrimal canal. Details of the medial surface of the lacrimal are unknown.

Dorsally, the prefrontal (Figs 2, 3, 7, 8) is anteriorly pointed and forms part of the interdigitating frontal/prefrontal-nasal suture. The blunt posterior end is angular in BMNH R3592 (Fig. 8), but more rounded in BPI 5207 (Fig. 2D) and NM QS1473 (Brink 1955). The dorsal surface is shallowly concave and sculptured with a curious pattern of shallow labyrinthine canals, most clearly seen in BMNH R3592 and GHG AK82–22. These canals are present on most of the dorsal surface of the skull roof, but are notably concentrated towards the lateral edge of the prefrontal. They bear a slight resemblance to the less extensive canals present on the dorsolateral margin of the prefrontals of *Sphenosuchus acutus* (Walker 1990).

The lateral edge of the dorsal part of the prefrontal is thickened, particularly posteriorly, to form a prominent overhanging brow. Running longitudinally on the posteroventral part of this ridge is a narrow groove, clearly seen in BMNH R3592 (Fig. 8B) and BPI 5207 (Fig. 2). Ventrally, this thickened area of bone ends in an abrupt step marking the lateral limit of a pronounced depression on the ventral surface of the skull roof in the area of nasal, frontal and prefrontal contact (Figs 7A, 8C).

The prefrontal pillar forms the anterior border of the orbit and articulates with the lacrimal. Its ventromedial extent is currently unknown.

The frontals (Figs 2, 7, 8) exist as paired, unfused elements forming the major part of the skull roof. They are broad posteriorly and narrow anteriorly, where long interdigitating

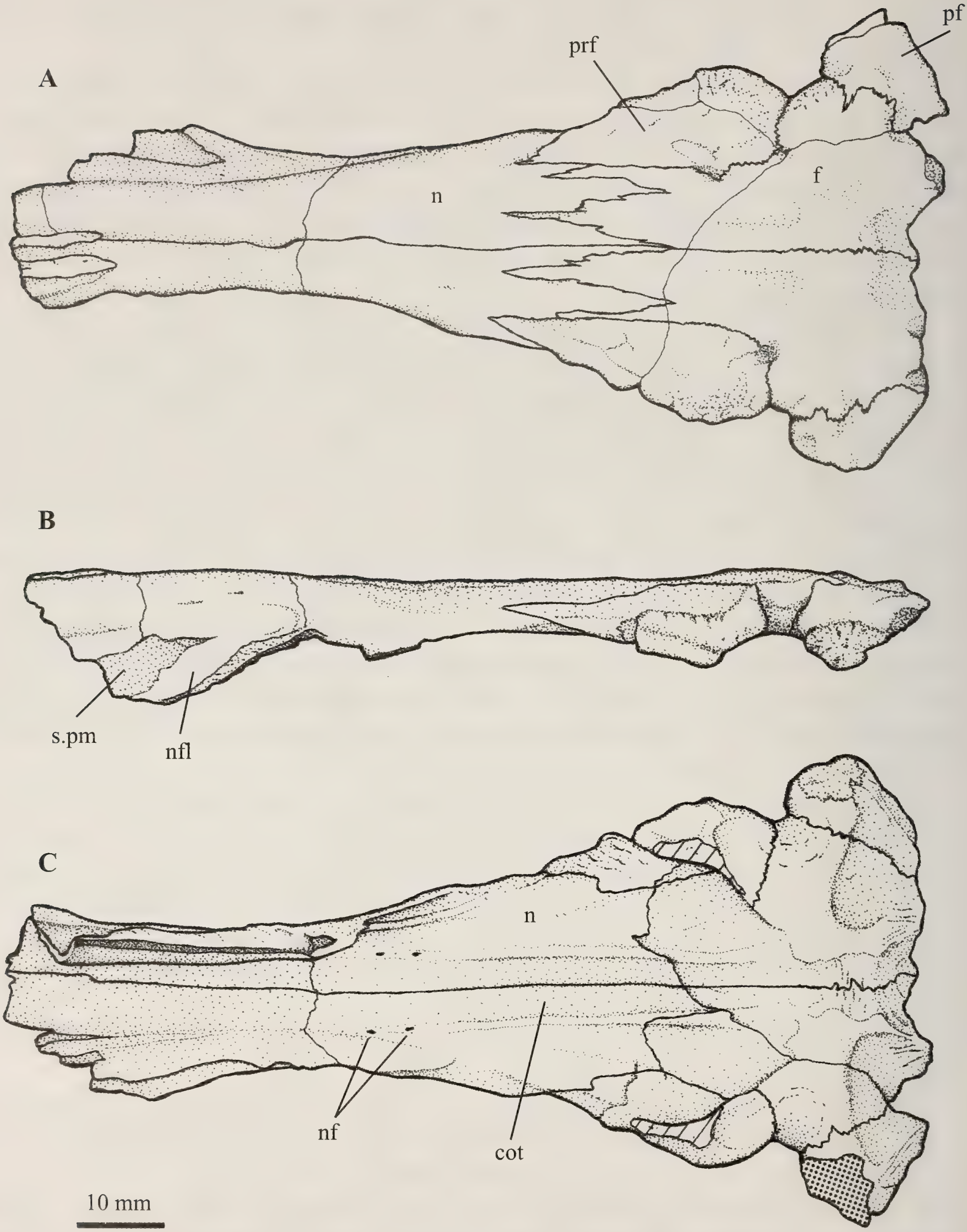

Figure 8

Erythrosuchus africanus, skull roof of BMNH R3592. A. Dorsal view. B. Left lateral view. C. Ventral view.

processes are sandwiched between the nasals, ventrally, and the prefrontals, dorsally. The frontals form part of the short dorsal border of the orbit—at the point where contact is made with the posterior part of the prefrontals. The opposite frontals meet at a well-defined midline suture that is anteriorly simple, but posteriorly weakly interdigitating. Weakly interdigitating sutures are also present at the point of frontal-parietal and frontal-postfrontal contact. The only well-preserved frontal-parietal suture (NM QS1473, Fig. 7A) is slightly curved. No contact is made between frontal and postorbital on the dorsal surface of the skull roof. The dorsal surface of the anterior of the frontals is essentially flat, but posteromedially they form the anterior limit of a steep-sided subrectangular depression that extends back on to the parietals. This is the 'pineal fossa' described by Parrish (1992).

The centre of the ventral surface of the frontals bears a posterior continuation of the channel for the olfactory tract (Figs 7A, 8C). The posterior limit of the midline frontal suture lies in an additional channel that broadens out as it extends back on to the parietals. Shallow depressions border the dorsal margins of the orbits on the ventral surface of the frontals of BMNH R3592 (Fig. 8C), and possibly GHG AK82–22 (absent in NM QS1473). The posterolateral part of the ventral surface of each frontal bears a large depression that is steep-sided and extends on to the postfrontals, postorbitals, and parietals. Only the posterior limits of these depressions receive the capitate processes of the laterosphenoids. Ventral contact between the frontal and postorbital excludes the postfrontal from the posterodorsal border of the orbit.

The postfrontal (Figs 2, 7, 8) is a small element that is tightly bound between the frontal, postorbital, and parietal. Dorsally it contributes to the posterodorsal border of the orbit. Much of the lateral border of the prefrontal is enveloped by the postorbital, and posteriorly brief contact is made with the parietal. The ventrolateral edge of the postfrontal is thickened, and the thinner posteromedial edge contributes to the depression that articulates with the capitate process of the laterosphenoid. In NM QS1473 only a small area of the postfrontal is exposed ventrally (Fig. 7A), and here it no longer contributes to the border of the orbit, although contact with the parietal is maintained.

The opposite parietals (Figs 2, 7–9) are firmly articulated but suturally distinct. They are short, fairly broad, and have well-developed posteroventral transverse processes. Laterally, and behind where contact is made with the frontals, postfrontals, and postorbitals, the thickened edges of the parietals form the medial borders of the supratemporal fenestrae. The central parts of the parietals are much thinner and bear the posterior extension of the pineal fossa back from the dorsal surface of the frontals. There is a fairly large and slightly irregular hole in the centre of this fossa in BMNH R3592 (Fig. 9D). Huene (1911) believed this to be a pineal foramen-a plesiomorphic feature for archosauromorphs—but doubt has been cast on the naturalness of this hole by subsequent workers (Charig & Reig 1970; Parrish 1992). Brink (1955) and Parrish (1992) reported the absence of a pineal foramen in NM QS1473 and Parrish (1992) also reported its absence in BPI 5207. Following an examination of all of these specimens, it is reported here that the hole in BMNH R3592 has become slightly larger and more irregularly shaped since it was last figured (Huene 1911, fig. 1). It is also positioned somewhat

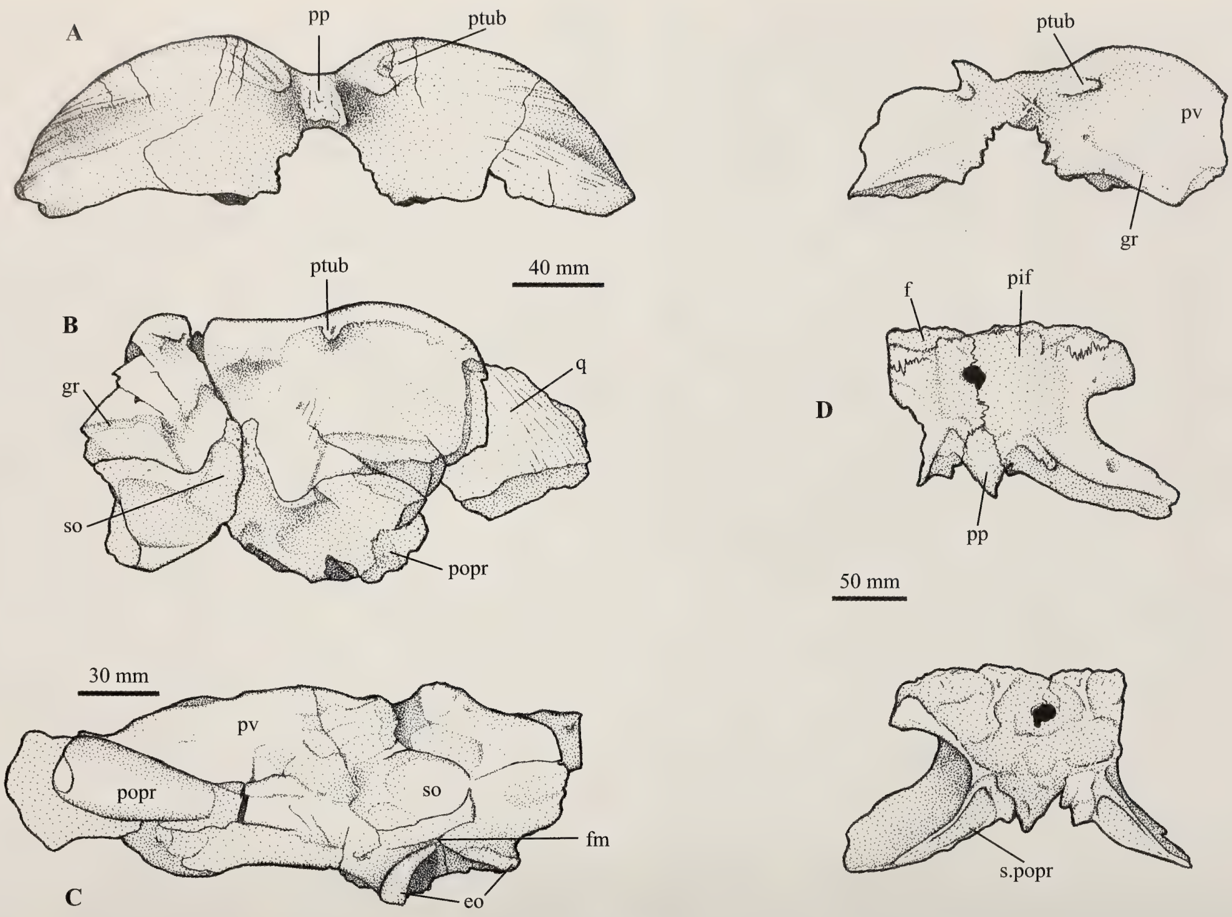

Figure 9

Erythrosuchus africanus, posterior part of the skull roof. A. NM QS1473 in occipital view. B. BPI 4645 in occipital view. C. BPI 4680 in occipital view. D. BMNH R3592 in occipital, dorsal and ventral views.

off-centre with respect to the midline suture. It was not possible to determine whether a small pineal foramen might present in NM QS1473 because of some restoration in this region of the specimen. The skull of BPI 5207 was compressed laterally during preservation and this means that the possible presence of a small foramen can not be discounted. BPI 3893 was incompletely prepared in this area at the time of this study, but is also laterally crushed here. In short, conclusive evidence on the presence or absence of a pineal foramen in *Erythrosuchus africanus* is not currently available.

The tall and broad occipital surface of each posteroventral transverse parietal process is essentially smooth, although two notable features are a dorsomedially positioned tubercle and, nearer the ventral edge, a subhorizontal transverse groove (Fig. 9). The dorsolateral edge of the occipital surface of the process of NM QS1473 (Fig. 9A) bears horizontal striations. The ventral surface of the process holds a well-defined and triangular-shaped socket for articulation with the dorsomedial edge of the paroccipital process. This articulation results in a post-temporal fenestra that was, at most, a narrow slit. The ventromedial edges of the transverse processes present a smoothly convoluted surface (BMNH R3592) for articulation with the supraoccipital.

The ventral surface of the roof of the parietals closely matches the dorsal contours of the laterosphenoids. Anteriorly there are small triangular ventral processes that rest between the capitate and anterior processes of the laterosphenoids. Longitudinal grooves on the ventral surface of these parietal processes form the dorsal surface of an 'anterodorsal channel' (see Gower & Sennikov 1996*b*; Gower 1997). A well-defined ventral concavity surrounds the central hole in the parietals of BMNH R3592. This area has been partially restored in NM QS1473.

The small postparietal (Figs 2, 7–9) is firmly sutured to the parietals, and projects posteriorly as a short, free-standing pyramidal peg—a feature possibly restricted to erythrosuchids (see also Gower & Sennikov 1996*b*). Its tapered anterior end is wedged between the posterior end of the parietals, and contact is also made with the supraoccipital ventrally.

The postorbital (Figs 2, 3, 7) is an unevenly triradiate bone. Its short anterior arm articulates with the anterolateral and posterolateral margins of the postfrontal, as well as the anterolateral edge of the parietal. The postorbital therefore excludes the postfrontal from the supratemporal fenestra (Figs 2C, 7A). As pointed out by Charig & Reig (1970), this arrangement is contrary to that reconstructed by Huene (1911). The postorbital makes a small contribution to the ventral depression for the capitate process of the laterosphenoid. The anteroventral portion of the anterior arm of the postorbital is laterally thickened and this contributes to an overhanging ridge at the posterodorsal corner of the orbit. A distinctive depression lies just behind and above this thickened area.

The posterior process of the postorbital is slightly arched and pointed seen in lateral view, and it articulates with a deep notch in the squamosal. The lateral surface of the distal end bears a narrow, slit-like groove (Fig. 2). This groove, clearly visible in both specimens where this area is preserved (BPI 5207 and 3893, NM QS1473), is accentuated by laterally raised borders. Parrish (1992) listed deep tongue-in-groove articulation between postorbital and squamosal as an erythrosuchid synapomorphy. The incised groove

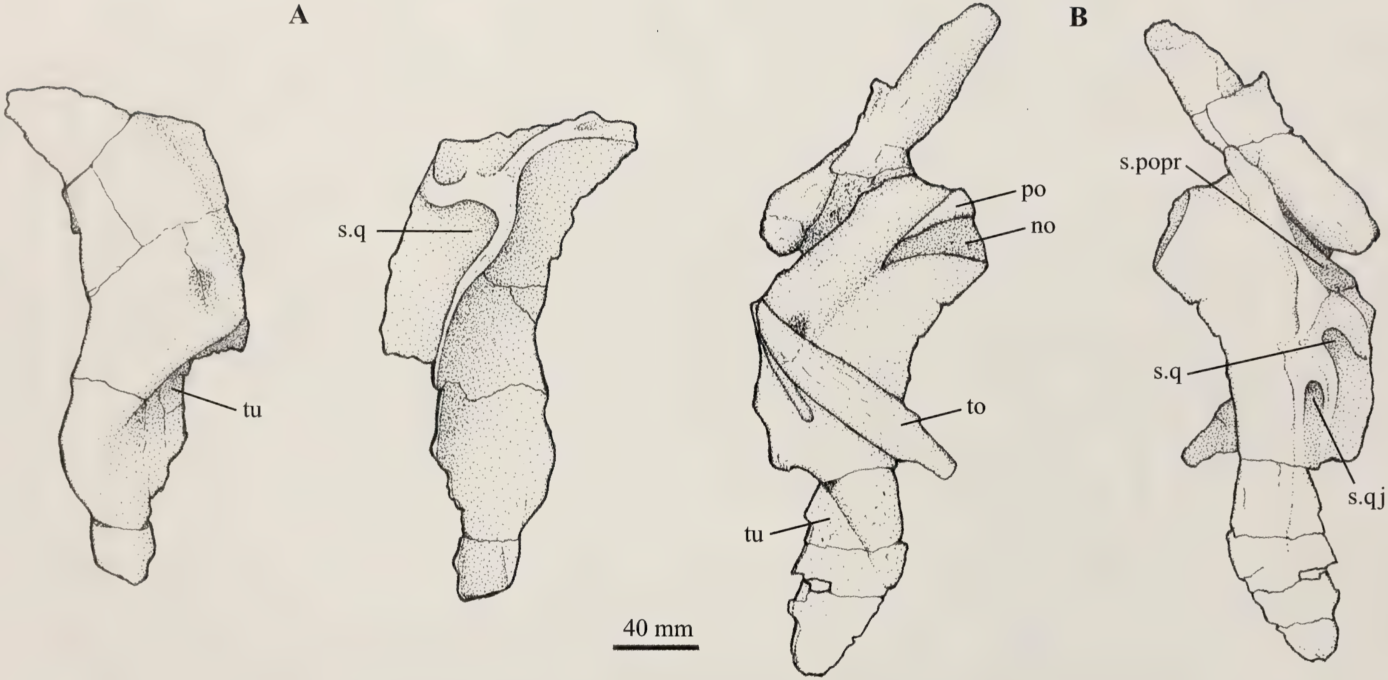

Figure 10

Erythrosuchus africanus, squamosals of BPI 4680. A. Lateral and medial views of left squamosal. B. Lateral and medial views of right squamosal.

described here reflects a deep contact and might contribute to a clearer definition of a more satisfactorily discrete character state.

The descending ramus of the squamosal (Figs 2, 10) is much longer than the anterior one. Towards its ventral edge the posterior margin of this ramus bears a laterally overhanging pleat or tuck (Fig. 10). This overhanging part forms a free-standing posterior edge that sheaths laterally the dorsal part of the quadrate. The part of the squamosal that is overhung continues ventrally to articulate with a depression on the lateral surface of the quadratojugal. This squamosal pleat is perhaps restricted among the earliest archosaurs to the erythrosuchids *Erythrosuchus* and *Shansisuchus* (personal observation of IVPP material). The ventral process of the squamosal of *E. africanus* extends down towards the posterior process of the jugal, and almost (BMNH R3592, BPI 4680) excludes the quadratojugal from the border of the lateral temporal fenestra.

The medial surface of the squamosal is complex and articulates with the parietal, paroccipital process of the opisthotic, the head of the quadrate, and the quadratojugal via a series of concavities (Fig. 10).

The anterior process of the jugal (Figs 2, 3) is excluded from the border of the antorbital fenestra. The dorsal edge of this same process forms the short ventral margin of the orbit, which is smoothly notched by a small and rounded, jugal projection (Fig. 2B). The anteroventral part of the anterior jugal process intimately interlocks with the maxilla. The anterior extremity of the jugal consists of a medial overhanging projection and a thin lateral flange, either side of a central ramus. The lateral flange is received by the gap between the lateral and medial parts of the maxilla (described above), and the medial projection articulates with the medial surface of the maxilla. This arrangement is also seen in *Proterosuchus fergusi* (personal observation of RC 96), and possibly has a broad distribution among early archosaurs.

The posterior process of the jugal is the longest, and forms the almost straight ventral border of the lateral temporal fenestra, with the medial surface of the process contacting the quadratojugal for most of its length. The anterior part of the articulation with the quadratojugal is simple, with the medial face of the jugal contacting the lateral wall of the quadratojugal. Posteriorly, however, the jugal tapers to a point and rests within a deep notch on the quadratojugal. The quadratojugal (Figs 2, 11) is a complex element that articulates with the jugal, squamosal and quadrate to form a robust posterolateral corner to the dermatocranium. The bone consists of three main rami: laterally compressed anterior and dorsal processes, and a more dorsoventrally compressed and anterodorsally inclined posteromedial process.

The anterior process articulates with the ventromedial surface of the jugal, continuing a long way forward as it does so, but never contributing to the ventral border of the lateral temporal fenestra. The posterior part of the quadratojugal extends back from the dorsal arm for a short distance, but it is largely expressed as a medial process that overlaps the base of the quadrate posteriorly (Fig. 11A). This configuration of the quadratojugal contributes to a large posterolateral and dorsal concavity in the lower posterolateral corner of the skull, lateral to the lower half of the quadrate.

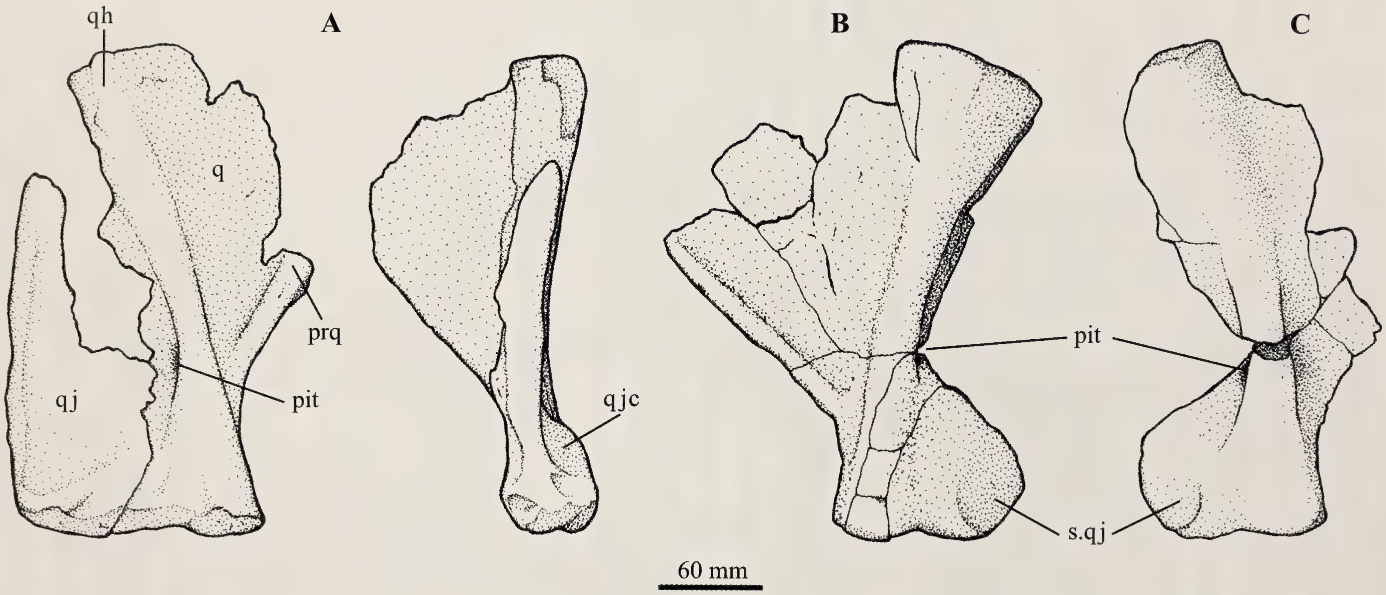

Figure 11

Erythrosuchus africanus. A. Posterior and lateral views of left quadrate and quadratojugal of BMNH R3592. B. Posterior view of right quadrate of BPI 4680. C. Posterior view of left quadrate of BPI 4680.

Palatal complex

The palate is the poorest known part of the skull. Information is available from incompletely prepared and/or disarticulated and fragmentary specimens only. The palatal contributions of the premaxilla and maxilla are described above.

The vomer of *Erythrosuchus africanus* is currently unknown. It should be preserved, but is currently not visible, in the specimens BPI 5207 and BPI 3893. The only clue to its form may come from the close resemblance (personal observation) of the other known palatal elements to those of *Garjainia prima* (Ochev 1975).

The palatine is currently known from a single incomplete example belonging to the left side of BMNH R3592 (Fig. 12), and a glimpse afforded by the anteriormost transverse section of BPI 3893 (Fig. 3C, D). The BMNH R3592 example is the bone described and figured by Huene (1911) as a vomer. Ochev (1975) interpreted this bone as a palatine, and it very closely resembles that element in *Garjainia prima* and *Vjushkovia triplicostata* (Ochev 1975; personal observation). It is very different from the long, slender, and strongly dorso-ventrally compressed palatines of, for example, *Proterosuchus* (Cruickshank 1972) and *Prolacerta broomi* (Gow 1975). It is constructed of thin lamellae—a lateral one articulates with the maxilla, and a medial one with the pterygoid. These meet near the anterior end of the palatine but they diverge posteriorly—contact being maintained between the two by a third, more horizontal lamella. The horizontal lamella and part of the medial one form part of the roof of the mouth.

The lateral lamella is essentially flat on its outer face, although centrally it bears a narrow triangular depression. Anteriorly, the incomplete lamella seems to be tapering to a point and, just behind this, the medial lamella joins it. A thickened and subcylindrical dorsal process is present at the point where these two lamellae meet. The notch between the anterior edge of this process and the dorsal part of the anterior extension of the lateral lamella, forms the posterior border of the choana. Both the dorsal process and the thin medial lamella probably continued upwards and forwards, as in *Garjainia prima* and *Vjushkovia triplicostata* (Ochev 1975), to contact the posterior end of the vomer as well as the anterior of the pterygoid. A small area anterior to this is irregularly roughened and bears two circular pits. It is unclear if these are simply irregular growths or likely to be characteristic for the species. It seems unlikely that this pitted, roughened area was associated with palatal teeth.

Palatal teeth are present in at least one erythrosuchid, based on a re-examination of the palatines of *V. triplicostata*. One of these, PIN 951/18, was incorrectly described by Ochev (1975) as a left-side element. Contrary to Ochev, the palatines of *V. triplicostata* clearly exhibit a number of small, blunt, conical teeth as well as some empty pit-like 'sockets'. This is the first report of the presence of palatal teeth in erythrosuchids. Palatal teeth are known in proterosuchids (e.g. Cruickshank 1972; Gower & Sennikov 1997; Welman 1998), but their absence was previously thought to have characterized the clade consisting of all archosaurs other than proterosuchids (e.g. Benton & Clark 1988; Sereno 1991; Parrish 1992). Although the pits on the palatine of BMNH R3592 approximately resemble the empty 'sockets' in *V. triplicostata*, a similarly rough and pitted surface is seen on some non-palatal elements of the BMNH R3592 material (e.g. anterior fragment

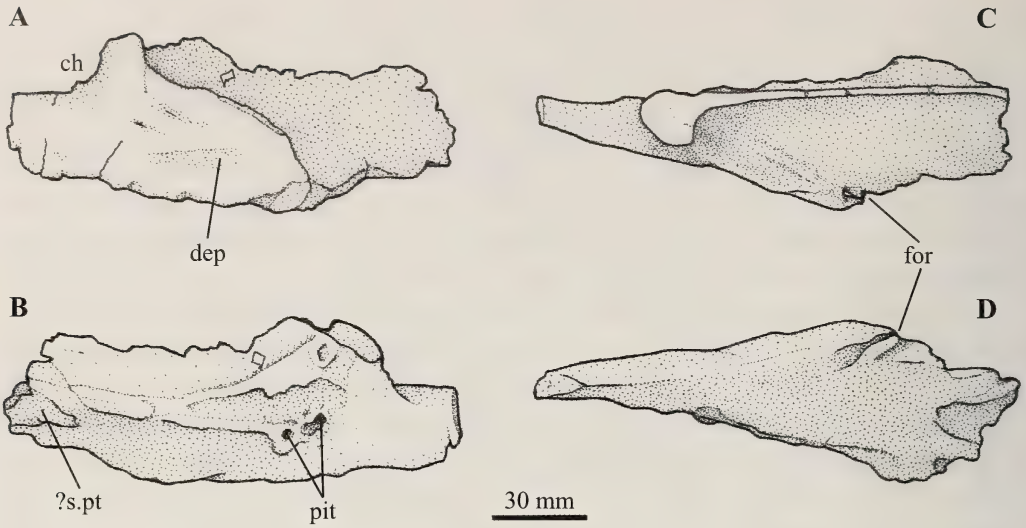

Figure 12

Erythrosuchus africanus, left palatine of BMNH R3592. A. Lateral and slightly dorsal view. B. Ventrolateral view. C. Dorsomedial view. D. Medial and slightly ventral view.

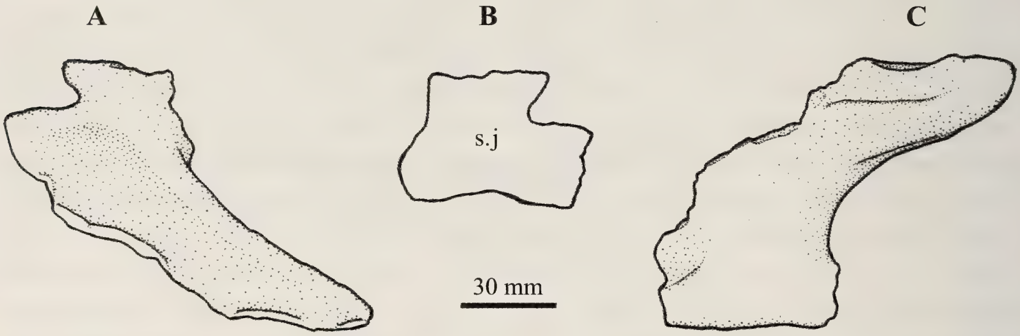

Figure 13

Erythrosuchus africanus, right ectopterygoid of BPI 4680. A. Medial view. B. Lateral view. C. Ventral view.

of left jugal). Furthermore, the pits on the palatine of BMNH R3592 are few in number and relatively rather large.

At the point where the central lamella meets the lateral lamella, two foramina pass between the floor of the dorsal hollow and the ventral edge of the palatine. The palatine of *Garjainia prima* also exhibits a foramen in this region (Ochev 1975, fig. 3). A low and weakly defined ridge extends anteromedially along the floor of the dorsal hollow, from a position just anterior to the complete foramen.

The palatine is also visible in the anteriormost section through BPI 3893. Details are

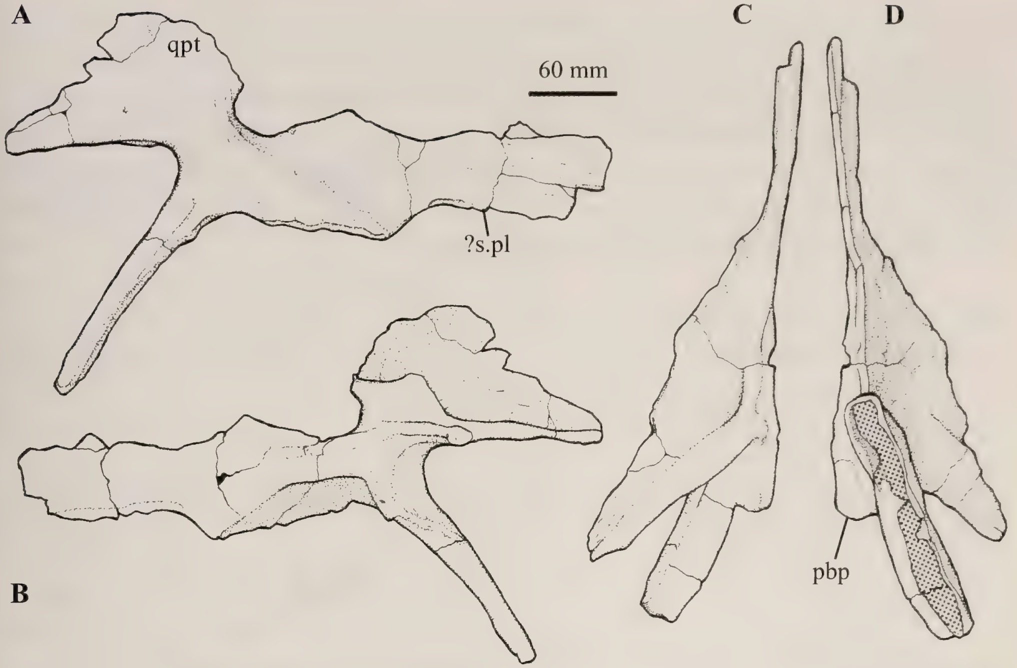

Figure 14

Erythrosuchus africanus, right pterygoid of BMNH R3592. A. Lateral view. B. Medial view. C. Ventral view. D. Dorsal view.

hard to interpret, partly due to the angle of the section, but Figures 3C and D shows the palatine contacting the ventrolateral edge of the pterygoid and articulating with the medial maxillary wall. Evidence for this also comes from the medial 'scars' seen on some of the maxillae (see above). This specimen, and comparison with *G. prima* (Ochev 1975), indicates that the opposite palatines probably did not meet along the midline.

Most of the information on the morphology of the ectopterygoid comes from single examples from BPI 4680 (Fig. 13) and BMNH R3592, both from the right side. The articular surface for the jugal is subquadrangular with an anterior notch (Fig. 13B). It is almost certain that the ectopterygoid did not contact the maxilla in addition to the jugal. A substantial tapering process stems from the articular head and extends posteriorly, medially, and ventrally. The medial margin is incomplete in both examples but would have articulated with the lateral margin of the ventrolateral ramus of the pterygoid. The dorsal surface of the proximal part of the tapering posterior process bears a distinct depression—giving this part of the ectopterygoid a concavo-convex transverse section. The anterior margin is incomplete in both examples so that there is no indication of the form of the posterior border of the suborbital fenestra. The BMNH R3592 example is less well-preserved, slightly distorted, and was not identified or described by Huene (1911). The only other direct information on the morphology of the ectopterygoids comes from a glimpse through the right lateral temporal fenestra of BPI 5207 (Fig. 2B), which shows the

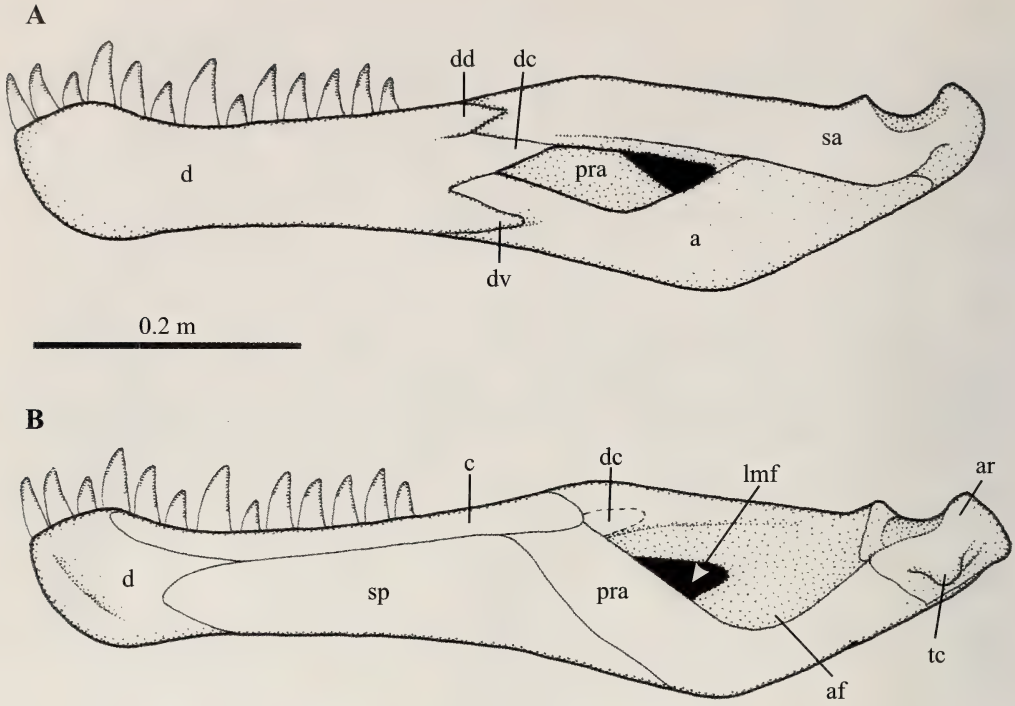

Figure 15

Erythrosuchus africanus, restorations of the mandible. A. Lateral view. B. More speculative medial view. The text should be consulted for information on the confidence that can be had in these restorations.

posterior part of the head of the ectopterygoid articulating with the medial surface of the jugal, and one of the transverse sections through the skull of BPI 3893 (Fig. 3E, F).

The form of the ectopterygoid, with an articular head and a long posterior process that extends to the end of the ventrolateral ramus of the pterygoid, is essentially the same as in *Proterosuchus* (Cruickshank 1972) and *Garjainia prima* (personal observation). Re-examination of PIN material shows that Ochev (1975) misidentified the distal end of the posterior process of the ectopterygoid of *G. prima* as a thickened ventrolateral pterygoid edge.

The pterygoids (Figs 2, 3, 14) are deep and narrow elements. It is unclear how far forward the dorsally arched palatal ramus extends but, in the light of many other close similarities to the palate of *G. prima* (Ochev 1975), it is probable that contact was made with the posterior of the vomer. The posterior edge of the ventrolateral process is considerably thickened and almost cylindrical. Most of its lateral edge would have contacted the ectopterygoid.

In lateral view the quadrate ramus appears as a large, smooth and triangular-shaped surface, whereas medially it can be seen that it is trough-like in form, with a low medial wall. The floor of this ‘trough’ articulates with the pterygoid process of the quadrate. The basal articulation is seen as a roughened and possibly incomplete oval surface on the end of a horizontal ridge on the medial face of the central body of the pterygoid (Fig. 14B). The sections through the skull of BPI 3893 (Fig. 3) show that an interpterygoid vacuity was present along most of the length of the pterygoids. This becomes steadily narrower anteriorly, and is eventually lost as the pterygoids appear to make contact along the midline (Fig. 3D). There are no teeth on any part of the pterygoid. As Ochev (1975: 102) realized, Huene (1911: 10, pls 1, 7) turned the right pterygoid of BMNH R3592 upside down and referred to it as the left.

The quadrate of *Erythrosuchus africanus* is quite well known. It consists of a ventral condylar area, a subvertical central ridge and an anteromedial lamella. The central ridge of the quadrate (Fig. 11) is slightly bowed in lateral view. The base is expanded laterally to provide a shallow depressed area for articulation with the medial arm of the quadratojugal. The ventral surface of this area forms a kidney-shaped condyle. Just above the depression for the quadratojugal, and about one-third up the height of the quadrate, is a posterolaterally facing pit. This was described by Huene (1911) as the quadrate foramen but it is a blind hollow, similar to a closed pit in the same position in *Sphenosuchus acutus* (Walker 1990). The quadrate of *Stagonolepis robertsoni* has a blind pit lying medial to an open foramen (Walker 1961).

The quadrates of BMNH R3592 and BPI 4680 are incompletely preserved along their lateral edges, but they present no evidence for the presence of a large quadrate foramen. BPI 5207 shows minimal lateral compression here, and confirms that a quadrate foramen was absent in *Erythrosuchus africanus*. Although absent in some species, e.g. *Sphenosuchus acutus* (Walker, 1990), the quadrate foramen is a persistent feature present in many fossil archosaurs, including proterosuchids (e.g. Cruickshank 1972; Gower & Sennikov 1997), *Garjainia prima* (Ochev, 1981), *Euparkeria capensis* (Ewer, 1965), aetosaurians (e.g. Walker 1961), and rauisuchians (Gower 1999).

Epipterygoids are not clearly visible in any specimen. A glimpse of the epipterygoid through the right lateral temporal fenestra of BPI 5207 (Fig. 2B) shows that it was similar in structure to those of other non-crown-group archosaurs (e.g. *Garjainia prima*—Ochev 1975; *Proterosuchus*—Cruickshank 1972; Clark *et al.* 1993), in having a broad base that contacts the dorsal part of the pterygoid, and a slender dorsal process.

MANDIBLE

The lower jaw is fairly well known except for some details of the medial surface. It is composed of seven elements and there is a well-developed lateral mandibular fenestra. A reconstruction in lateral and medial view is shown in Figure 15. The reconstructed lateral aspect is considered to be accurate, but medial details of the area of prearticular-dentary-splenial-coronoid contact remain poorly known and are more speculatively reconstructed.

The anterior of the dentary is dorsoventrally expanded (Fig. 2). As has been suggested for crocodylomorphs exhibiting a similar condition (Parrish 1991; Sereno & Wild 1992), the upturning of the anterodorsal margin of the dentary may be a developmentally more

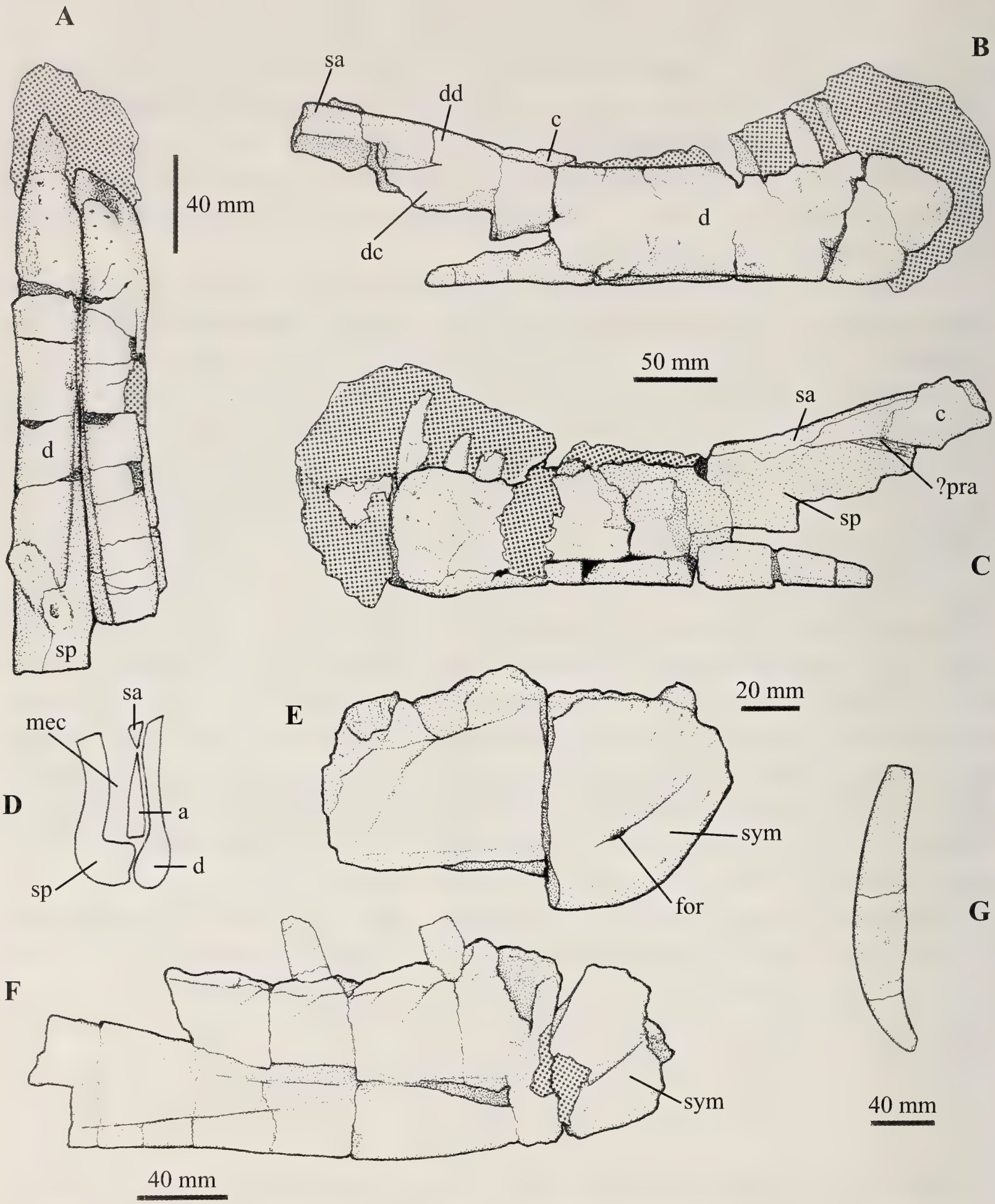

Figure 16

Erythrosuchus africanus. A. Anterior part of the mandible of BPI 3893 in ventral view. B. Anterior part of the mandible of BPI 3893 in right lateral view. C. Anterior part of the mandible of BPI 3893 in left lateral view. D. Posterior view of section through right ramus seen in A. E. Medial view of right dentary of BMNH R3592. F. Medial view of right dentary of BMNH R2790. G. Isolated tooth of BMNH R3592.

consistent feature than any accompanying dorsoventral expansion of the distal end. Among non-crown-group archosaurs, however, this feature may be restricted to erythrosuchids.

Posteriorly, the dentary divides into three processes that taper to points (Fig. 2). The uppermost process articulates with a notch on the lateral surface of the surangular. The central process is marginally the largest and is directed slightly medially as well as posteriorly—so that it is wedged between the lateral surface of the angular and the medial surface of the surangular. The ventral edge of this process forms the anterodorsal border of the lateral mandibular fenestra. The lower process articulates with the angular by overlapping it laterally and resting on a small shelf. This configuration is present in *Garjainia prima* (Ochev 1981; personal observation), and it might be common to a wide range of basal archosaurs. It also appears to be similar to that described for *Herrerasaurus ischigualastensis* (Sereno & Novas 1993). The only notable difference is the presence, in *H. ischigualastensis*, of a lateral ridge on the dorsal process. The condition in *Erythrosuchus africanus* is also similar to that of at least some Recent crocodilians (Iordansky 1973; personal observation), where the central of three dentary processes passes medial to the surangular. In crocodilians the dorsal process is much reduced and the central process is more intimately sutured to the surangular. The condition in *H. ischigualastensis* is therefore not unique (*contra* Sereno & Novas 1993: 469) apart from, perhaps, the lateral ridge.

The anterolateral end of the Meckelian canal tapers to a point level with the position of the fifth alveolus. The dorsomedial surface of the dentary bears an anteriorly tapering and step-like depression that possibly held an elongate coronoid. BMNH R2790 shows a series of parallel channels, presumably vascular, running back posteroventrally over this step.

The dentaries of BMNH R2790 and R3592 suggest that the splenial did not reach the symphisis, but terminated at a point level with the fourth or fifth tooth alveolus. BPI 3893 (Fig. 16) demonstrates that the splenial formed much of the ventral as well as the medial wall of the Meckelian canal, with the ventral contribution increasing posteriorly. Contact with the coronoid is made posterodorsally, but anteriorly the dentary would appear to lie between these two elements. Each dentary holds approximately 13 teeth.

Knowledge of the coronoid is far from complete. Direct evidence of its presence was found only in BPI 3893 (Figs 3, 16), where the coronoid can be detected as a sliver of bone on the dorsomedial edge of the mandible. This demonstrates that the coronoid was more extensive than a crescent at the anterodorsal border of the adductor fossa, but clear evidence for the limit of its anterior extension is lacking—it may even have extended far anteriorly, lying between the dorsomedial edge of the dentary and the dorsolateral edge of the splenial. In non-archosaurian archosauromorphs such as rhynchosaurs (e.g. Huene 1938) and *Prolacerta broomi* (Gow 1975), the coronoid does not extend far anteriorly alongside the dentary, and in living archosaurs it is a small crescent of bone (crocodilians—e.g. Iordansky 1973) or absent (birds—e.g. Baumel & Witmer 1993). There is evidence that the coronoid was long and slender in some extinct archosaurs, including the erythrosuchid *Garjainia prima* (Ochev 1981; personal observation), the proterochampsid *Chanaresuchus bonapartei* (Romer 1971), and the early crocodylomorph *Sphenosuchus acutus* (Walker 1990).

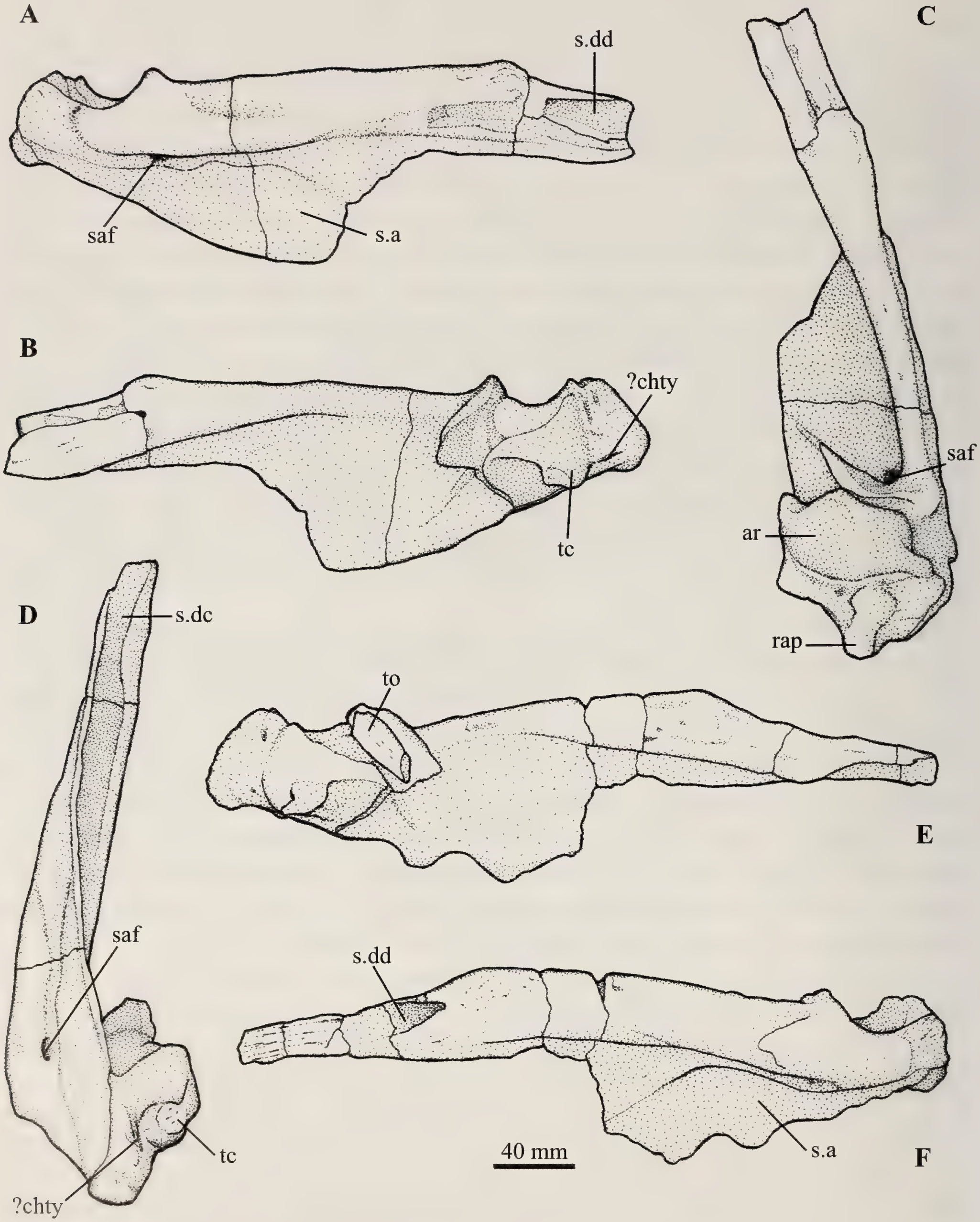

Figure 17

Erythrosuchus africanus, surangular and articular of BMNH R3592. A. Lateral view of right ramus. B. Medial view of right ramus. C. Dorsal view of right ramus. D. Ventral view of right ramus. E. Medial view of left ramus. F. Lateral view of left ramus.

The surangular (Figs 2, 3, 16, 17) is composed of a laterally-compressed posteroventral plate that is suspended from an angled longitudinal ridge. The tapered anterior end of the dorsal ridge bears a conspicuous notch (Fig. 17A, F) that receives the upper posterior process of the dentary. The central dentary process passes under the ventral edge of the anterior end of the surangular to contact the lateral face of a ventrally opening trough on the ventromedial surface of the surangular ridge. This area of the surangular has collapsed slightly during preservation in BPI 5207, so that it is expressed as a lateral depression (Fig. 2B).

Posteriorly, the dorsal ridge forms the lateral edge of the mandibular cotyle. A thin process extends anteromedially from the anterior margin of this area—its ventral edge maintains contact with the upper surface of the plate-like part of the surangular, and its posterior face firmly abuts against the anterior of the articular. Below the cotyle, the thickened part of the dorsal ridge ends abruptly in a stumpy posterolateral projection.

Most of the lateral face of the ventral plate of the surangular bears a shallow depression that receives the medial face of the posterior part of the angular. A large surangular foramen is seen laterally, below the anterior edge of the cotyle and under the overhanging dorsal ridge. A narrow and shallow groove extends anteriorly from this foramen, harboured by the overhang of the dorsal surangular ridge. The groove becomes slightly broader as it extends anterodorsally over the ventrolateral edge of the dorsal ridge, where it eventually disappears.

The articular (Fig. 17) is a thick bone that forms the major portion of the mandibular cotyle and retroarticular process. The cotyle is subdivided into two depressions by a slight, diagonal ridge. The anteromedial surface of the articular articulates with the posterior part of the lateral face of the prearticular. Behind this contact, the posteromedial surface of the articular bears a prominently projecting tubercle. A narrow channel running below this tubercle, and an associated foramen further up on the medial face of the retroarticular process (Fig. 17B, D), may have served to transmit the chorda tympani branch of the facial nerve. The low, rounded retroarticular process is formed by a small part of the surangular as well as the articular. Among the earliest archosaurs, it resembles that of *Shansisuchus shansisuchus* (personal observation of IVPP material documented by Young 1964) in that it lacks the free-standing, dorsally projecting process at the end of the retroarticular region present in *Garjainia prima* and proterosuchids (personal observation).

Current knowledge of the prearticular (Figs 2, 16) is also incomplete. The posterior end is forked and articulates with the articular and the ventromedial edge of the ventral lamella of the surangular. Most of the dorsal edge was free standing, and the ventral edge articulated with the angular, and probably contributed to the infra-Meckelian fossa. Very little is known of the anterior end of the prearticular, although a small piece of bone visible in BPI 3893 (Fig. 16C) suggests that it extended far enough anteriorly to rest between the posterior ends of the splenial and coronoid. Nothing is known of the lateral surface except a glimpse afforded through the right lateral mandibular fenestra of BPI 5207 (Fig. 2B).

The angular (Figs 2, 3, 18) articulates with most of the other mandibular elements. A small lateral shelf near the anterior end presents an area for articulation with the lower posterior process of the dentary. Posteriorly, the lateral face is dorsoventrally expanded,

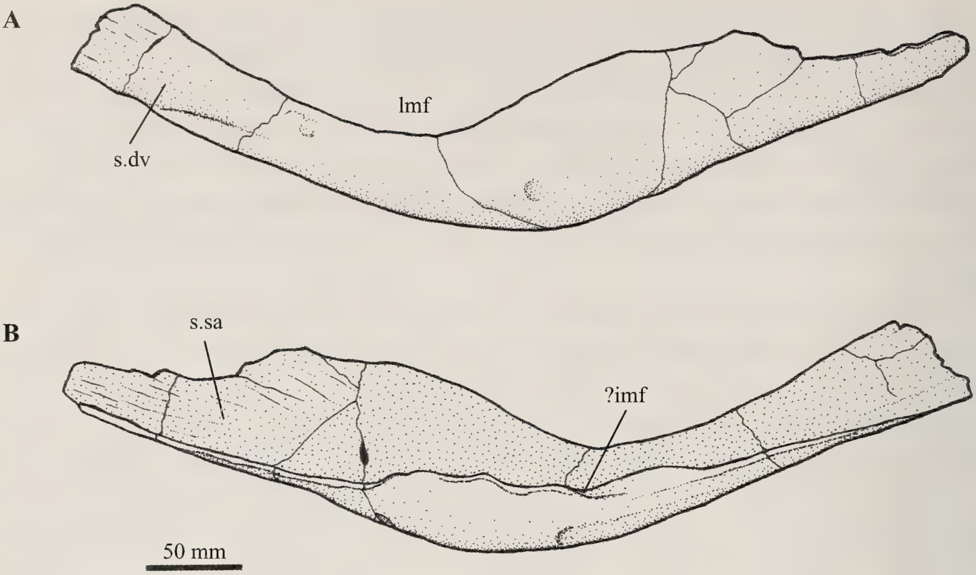

Figure 18

Erythrosuchus africanus, left angular of BMNH R3592. A. Lateral view. B. Medial view.

and it overlaps laterally a large area of the posteroventral lamella of the surangular and a small ventral part of the articular.

The central portion of the angular forms the floor of the large adductor fossa. A notch in the dorsal margin of the medial part (Fig. 18B) probably represents the position of the infra-Meckelian foramen—its margin being completed by the prearticular.

DENTITION

The marginal teeth of *Erythrosuchus africanus* (Fig. 16G) are typical of many carnivorous archosaurs in that they are large, laterally compressed, recurved, sharply pointed, and serrated. The mesial edge is more rounded than the sharply tapering distal margin, and the labial edge is more convex than the lingual one. The serrations on the distal edge extend from the pointed tip to the base of the crown, but mesially they extend for only half of the length from tip to crown. The teeth have long cylindrical roots that are embedded within sockets in the jaw. The bone at the edge of each alveolus of fully developed teeth is in close contact with the fully developed tooth surface, without approaching the condition seen in proterosuchids (see Gower & Sennikov 1997). Sections through the teeth show layered dentine surrounding a central lumen. There appears to be minimal variation in form throughout both the upper and lower jaw.

The premaxilla holds five teeth. The first three alveoli are fairly equal in size but the last two are markedly smaller, and are situated in the broad notch between the premaxilla and maxilla. The first maxillary tooth is similar in size to the last of the premaxilla. From here, there is an increase in tooth size posteriorly, up to a point where the maxilla is at its deepest and the largest maxillary tooth is held. The alveolar depth decreases steadily from here to the posterior end of the maxilla, but the size of the erupted crowns of the teeth is not noticeably reduced until the last few teeth, which are markedly smaller.

Knowledge of the mandibular dentition is far from complete. It is likely that the mandibular dentition did not oppose the first and last few teeth of the upper jaw. Potential variation in tooth size along the length of the dentary is unknown, because no specimen reveals enough information. It is probable that a general decrease in size occurred posteriorly, with the largest teeth being held by the deep anterior part of the dentary.

Tooth replacement in *Erythrosuchus africanus* occurred by the emergence of the new tooth in a position lingual to the functional tooth, with the alternate tooth replacement pattern seen in many 'thecodontian' archosaurs. The replacement teeth in the two sides of the upper jaw are out of phase. Evidence comes from the premaxilla of BMNH R3592 (Fig. 4C), where the right side has functioning teeth in the first and third alveoli but a replacing tooth in the second, and the left side has a replacing first tooth and a large functional second. Further evidence comes from BPI 5207 (Fig. 2), where large functioning third and fifth maxillary teeth border a smaller, replacing fourth tooth. The right maxilla of the same specimen shows the opposite situation.

VERTEBRAL COLUMN

Vertebrae and ribs

Only a few of the known specimens of *Erythrosuchus africanus* include vertebrae, and none exhibits a complete series. Furthermore, preservation and/or preparation is often imperfect, making the identification of the exact position of isolated vertebrae problematic. It has been possible, however, to discern most of the morphological characteristics associated with changes in serial position. These closely follow those known for other early archosaurs (Hughes 1963; Cruickshank 1972).

There are two sacral vertebrae and an estimated 25 presacral vertebrae, also the number in *Proterosuchus* (Cruickshank 1972) and as estimated for *Vjushkovia triplicostata* by Huene (1960). The almost complete tail of BMNH R3592 indicates that there were approximately 35 caudal vertebrae. All of the presacral vertebrae are notably short relative to their height, particularly in the pectoral region, and the centra are consistently taller than they are long throughout the presacral column. The centra are platycoelus to amphiplatyan and are laterally constricted or excavated. The dorsal neural arches are pierced by often complex, subdivided pits or foramina. These are perhaps pneumatic in nature (Gower 2001), but this requires further investigation because pneumatized vertebrae are generally considered to be restricted to more derived archosaurs (e.g. Britt 1994; Britt *et al.* 1998). Intercentra are present throughout the length of the precaudal column and three-headed ribs are present in the pectoral region.

It is probable that all of the precaudal vertebrae bore ribs. Unfortunately they are incompletely known, largely because articulated postcranial specimens have not been found. This is particularly true of the presacral ribs, where much of the information had to

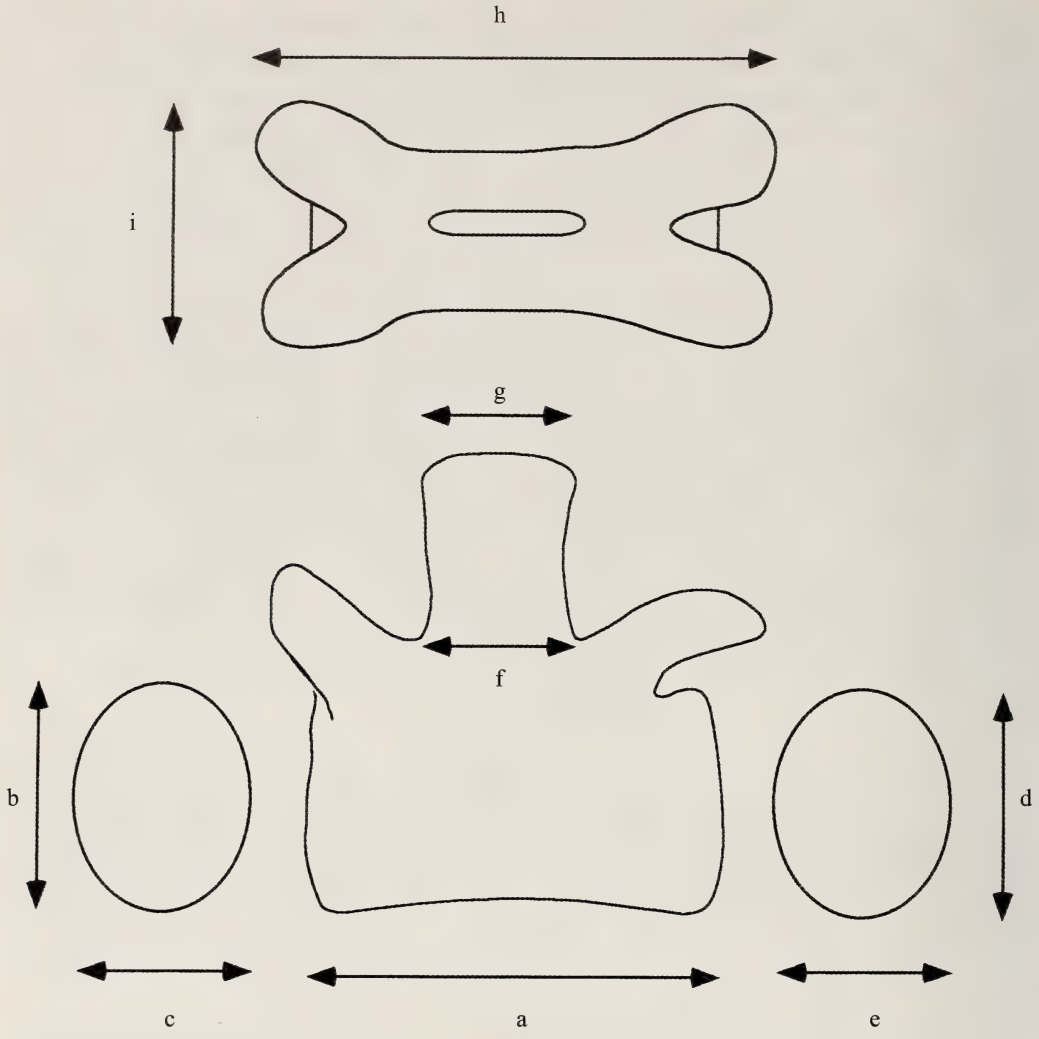

Figure 19

Diagrammatic views of vertebra showing dimensions recorded in Tables 1 and 2. a = centrum length; b = centrum height anteriorly; c = centrum width anteriorly; d = centrum height posteriorly; e = centrum width posteriorly; f = length of base of neural spine; g = length of distal end of neural spine; h = longitudinal distance between tips of zygapophyses; i = maximum transverse distance across anterior zygapophyses.

be gained from the corresponding articulatory surfaces on the vertebrae. The sacral ribs and most of the caudal ribs are well known. Measurements of a number of vertebral dimensions, defined diagrammatically in Figure 19, are presented in Tables 1 and 2.

Identification of a proatlas is uncertain. Squashed on to the lateral surface of the right atlas neural arch of BPI 4680 (Fig. 20A) is a slender splint of bone, similar in shape and relative size to the proatlas of *Euparkeria capensis* described by Ewer (1965). The presence of a proatlas in *Erythrosuchus africanus* is also suggested by an anterior

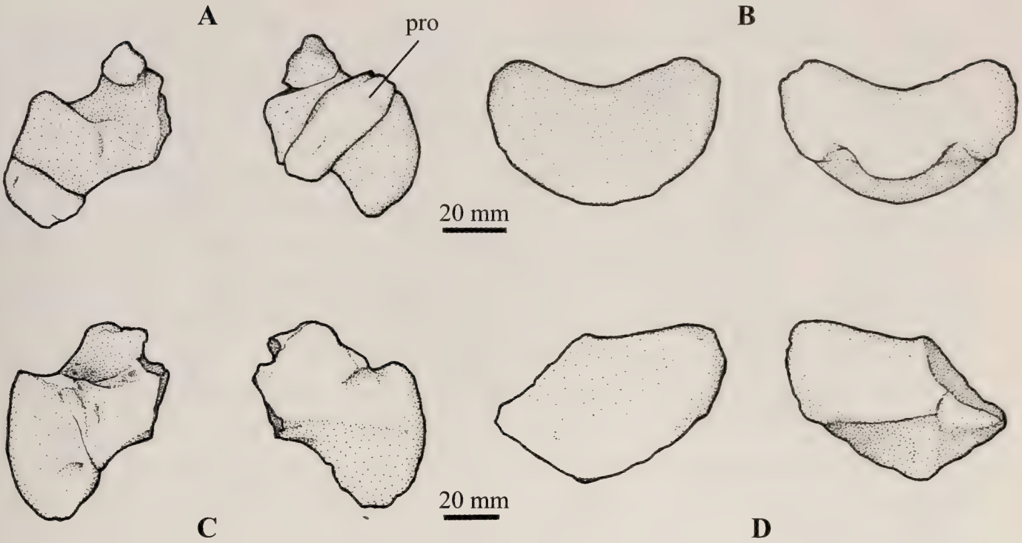

Figure 20

Erythrosuchus africanus. A. Medial and lateral views of right atlas neural arch of BPI 4680. B. Anterior and posterior views of atlas intercentrum of BPI 4680. C. Medial and lateral views of right atlas neural arch of BMNH R3592. D. Anterior and posterior views of atlas intercentrum of BMNH R3592.

projection on the atlas neural arch, articulatory facets on the exoccipitals, and by the presence of a proatlas in other early archosaurs.

The neural arch of the atlas (Fig. 20A, C) consists of a main body with a small anterior projection and a longer, tapering posterior process. The arches are paired and unfused, with the gap between them being partly overhung by the axis neural spine. The element as a whole is laterally convex and medially concave. The main part of the arch contacting the atlas intercentrum is short, broad, and transversely thick. The anterior edge forms an area for articulation with the occipital condyle. The anterior projection arises dorsally, just behind the anterior margin of the main body. It continues for a short distance anteromedially before contacting the proatlas. There are two hollows at the base of the anterior projection—anteromedially and posteriorly.

The intercentrum of the atlas is well preserved in BPI 4680 and BMNH R3592 (Fig. 20B, D) as a crescent-shaped wedge of bone very similar to that of *Euparkeria capensis* (Ewer 1965). Posteriorly the ventral edge is bevelled, and posterolaterally each side forms a single facet for articulation with what was probably a single-headed rib. The atlas centrum and axis intercentrum have not been identified or preserved in any currently known specimen.

The centrum of the axis (seen in BPI 5207, Fig. 21A) is short and unkeeled, and the anterior surface is perhaps more convex than in the other vertebrae of the column. The anterodorsal part of the lateral edge of the centrum is raised to form what is interpreted as a weakly expressed diapophysis. This facet is in a significantly more dorsal position than the diapophyses of the following cervical vertebrae, such as is also seen in *Proterosuchus*

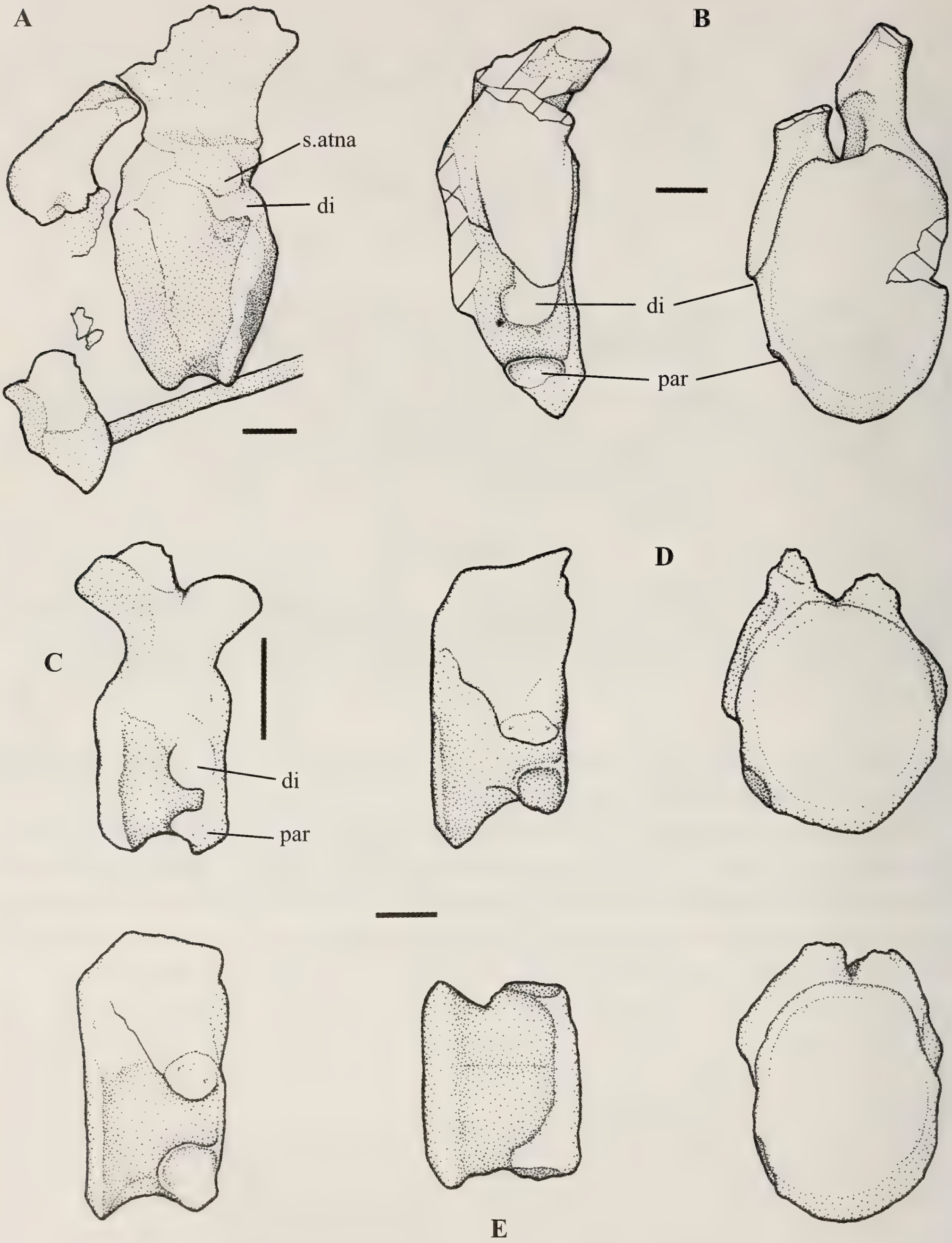

Figure 21

Erythrosuchus africanus. A. Right lateral view of axis and incomplete third presacral vertebra of BPI 5207. B. Right lateral and anterior views of third(?) presacral vertebra of BMNH R3592. C. Right lateral view of anterior cervical vertebra of SAM–3028. D. Right lateral and anterior views of cervical vertebra of BPI 4680. E. Right lateral, ventral and anterior views of slightly more posterior cervical vertebra of BPI 4680. All scale bars represent 20 mm.

(Broili & Schröder 1934). There is no indication of a parapophysis below this. The neural spine is incomplete but was clearly expanded. The atlas and axis ribs are unknown.

The anteriormost cervical vertebra might be represented by an incomplete example from BMNH R3592 (Fig. 21B; Hughes 1963). The centrum is much taller than it is long and bears circular parapophyseal and diapophyseal facets low down on its lateral surface. Other anterior cervicals (SAM–3028, BPI 4680—Fig. 21), have more circular faces to the centra, and the ratio between height and length is less (Table 1).

A number of changes in morphology occur in moving posteriorly along the cervicals and approaching the pectoral region (Table 1). The centra become taller, shorter longitudinally, and show increased lateral constriction. The articulatory surfaces become more circular in shape and the ventral margins remain bevelled. The parapophysis remains low down on the anterior edge of the centrum, but the facet becomes dorsoventrally elongated, whereas the diapophysis 'migrates' up the anterior edge.

BMNH R3592 includes two fairly well-preserved posterior cervical centra that, because of their distinctive morphology and the aforementioned problem of deducing their exact position, are referred to here as 'pectoral vertebrae'. They are described in some detail here because of the evidence they provide for the presence of three-headed ribs. The more posterior centrum (Fig. 22B) was artificially stuck to a complete neural arch and spine, and was considered by Charig & Reig (1970) to be a composite. Charig & Reig used this as evidence in rejecting Tatarinov's (1961) claim that facets for three-headed ribs could be identified in this specimen. The centrum and arch have since been separated. BMNH R3592 includes an additional disarticulated neural arch (Fig. 22C) and centrum that are similar in form to the equivalent components of the former composite example. The former composite arch fits this second, isolated centrum very closely, as does the free arch with the former composite centrum, and the interpretation here is that this was the original configuration. It is also suggested that these two vertebrae articulated directly with one another in the column, with the formerly composite centrum and isolated arch belonging to the more posterior (?ninth) of two consecutive vertebrae. In both examples, the centrum forms only a small part of the diapophysis, whereas the parapophysis remains low down on the anterolateral edge.

Although the two pectoral centra of BMNH R3592 share almost identical morphologies, the corresponding neural arches show some differences. The ventral processes of the more posterior arch (Fig. 22C) are much more prominent, more horizontally directed, and more sculptured than in the preceding example. The distal end of the diapophysis does not form a simple oval-shaped facet, but is instead constricted to present two quasi-discrete areas (Fig. 22C). The larger upper area is oval-shaped and its long axis leans back at approximately 45° to the vertical. The second area forms part of a smaller and more circular facet with the diapophyseal component of the centrum. This arrangement strongly suggests the presence of three-headed pectoral ribs very similar to those of *Vjushkovia triplicostata* (Huene 1960; personal observation). This is supported by the presence of three heads in a rib of *Erythrosuchus africanus* described below. BPI 4680 and SAM–PK–K10025 both include a number of fragmentary, crushed and isolated centra, that are posterior cervicals or possibly anteriormost dorsals. These are listed as pectorals in Table 1.

TABLE 1

Various dimensions of precaudal vertebrae in five specimens of *Erythrosuchus africanus*. The dimensions a–g are defined in Figure 19. AC = anterior cervical; CE = cervical; P = pectoral; D = dorsal; AMD = anterior/mid dorsal; MD = mid dorsal; MPD = mid/posterior dorsal; PD = posterior dorsal; S = sacral

Specimen	Estimated position	Dimensions (mm)						
		a	b	c	d	e	f	g
BMNH R3592 (large)								
AC	3	57	110	77				
CE		50	109					
CE		61	105		107	90		
P	8	58	123	101	122	105	32	
P	9	54	125	106	123	113	34	32
AD	12	65	118	97	114	93	42	
AMD	15	68	105	91	96	91	51	72
AMD	16	72	103	90	100	85	52	74
MPD	20	78	102	89			58	73
MPD	22	78	94	85	98	82	56	76
S	S1	72	97	85	100	75	42	45
S	S2	69	100	75	90	70	35	
BMNH R3592 (small)								
MD	16				85	65		
MD	17	62	82	59	76	59	39	
MD	18	61	86	62	79	64	42	
MD	19	56	83	64	78	64	42	
MD	20		77	64				
PD	24	62	79	68	79	65	45	
BPI 4680								
AC	3/4	48	76	66	81	69		
AC	4/5	59	82	64	86	70		
PC	7	41	87	80	84	80		
P	8	44	87	75	91	80		
P	9	41	92	77	93	78		
P	10		91	86				
AD	11	41	85	81	81	75	29	
AD	13		89	84	80	70	35	
AMD	14		77	75	74	70	37	
MD			74	67	65	62		
MD	19	59	80	65	78	60		
DO			78	69	67	68		
DO			69	68	66	62		
DO		55	66		68			

Specimen	Estimated position	Dimensions (mm)						
		a	b	c	d	e	f	g
SAM K3028								
AC	4/5	55	79	65				
SAM K905								
MD		62	90	73	95	85		
PD		71	90	73		73		
PD		69			95	73		
SAM Kun-no.								
AC		47			81	65		
CE		49	79	58	80	65		
CE		48	75	65		72		
P			74	77				
P		42	82		80	73		
AD		40	88	75				
AD			85					
AD		48	80			77		
DO		68						
DO		70						
DO		47	67	65				
DO		51	73					
DO		52	66	56				
DO		52	75					

Anterior dorsal vertebrae are represented by single but relatively well-preserved examples from BMNH R3592 and BPI 4680 (Fig. 23). The centrum is longer than those of the 'pectoral' vertebrae and the articulatory faces are not so circular. The neural arch is still distinct suturally from the centrum, but is more complex in form. The simple and single diapophyseal facet is situated on the end of a near-horizontal transverse process that is subtriangular in cross-section. A lamella extends between the di- and parapophyses, and additional lamellae extend from the base of the transverse process. One of these is the development of the anterior ridge extending on to the lateral surface of the anterior zygapophysis, whereas another extends posteroventrally to the posterior edge of the centrum. Finally, a moderately developed posterior ridge extends to a position just below the posterior zygapophysis. There are two deep pits where the bases of the anterior and ventral lamellae converge. A similar pit is also positioned between the anterior and posterior zygapophyses—at the dorsal edge of the base of the transverse process.

Moving posteriorly along the dorsal series there is a general increase in centrum length and a decrease in height (Table 1). All of the dorsal centra (Fig. 24) show strong lateral constrictions. The neural arch pits become more complex, with each main excavation housing a number of smaller ones separated by narrow lamellae (Fig. 24B). The anterior pit becomes large and occupies much of the concave anterior surface of the transverse process. Further posteriorly in the column, as the parapophysis migrates dorsally, the anterior pit again becomes shallow and simple. The ventral pit gradually becomes less

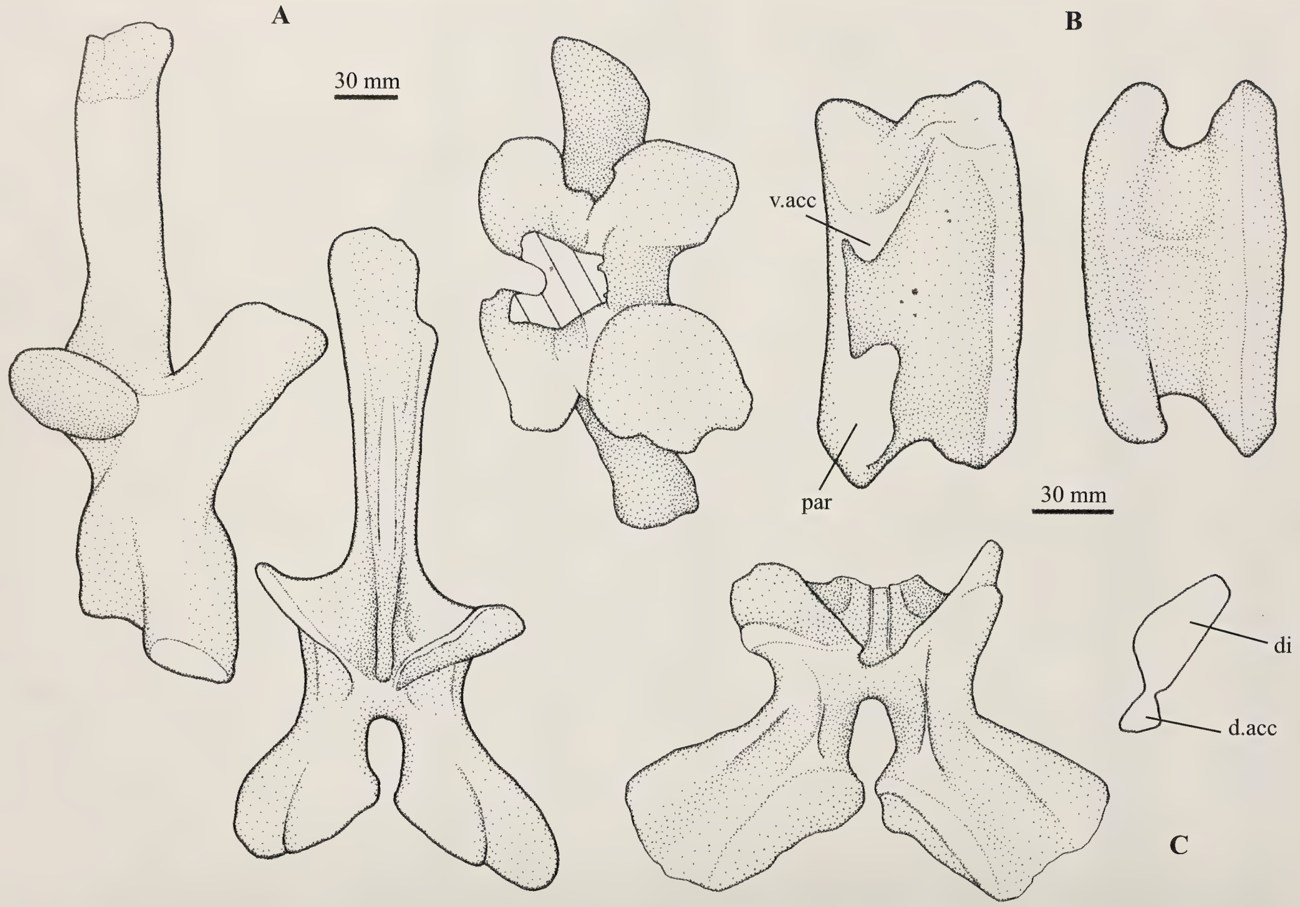

Figure 22

Erythrosuchus africanus, two consecutive pectoral vertebrae of BMNH R3592. A. Right lateral, posterior and dorsal view of more anterior neural arch. B. Left lateral and ventral views of more posterior centrum. C. More posterior neural arch in anterior view, plus outline of facets for left rib.

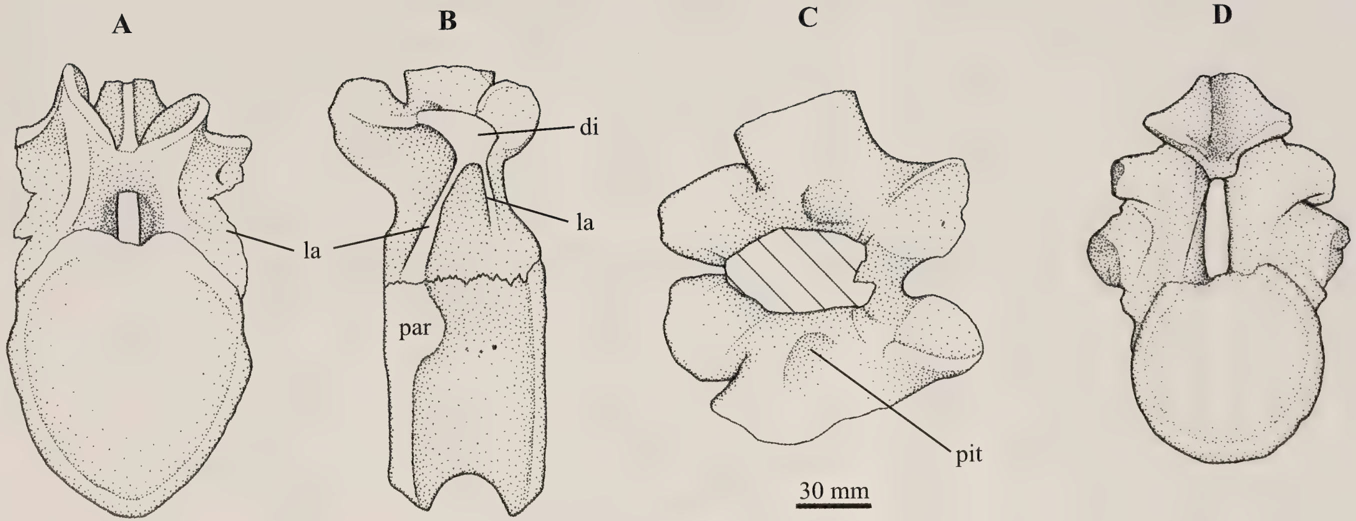

Figure 23

Erythrosuchus africanus. A. Anterior view of anterior dorsal vertebra of BMNH R3592. B. Left lateral view of anterior dorsal vertebra of BMNH R3592. C. Dorsal view of anterior dorsal vertebra of BMNH R3592. D. Posterior view of anterior dorsal vertebra of BPI 4680.

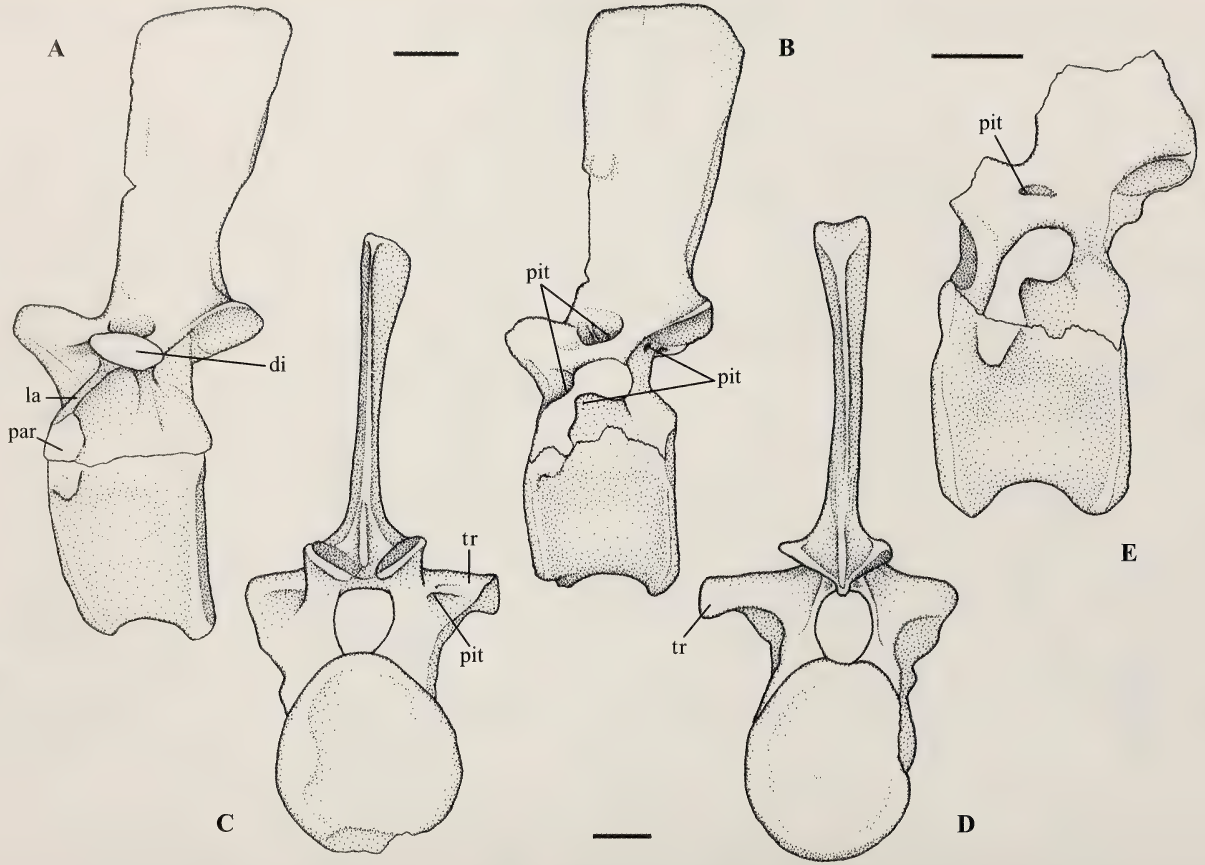

Figure 24

Erythrosuchus africanus, dorsal vertebrae of BMNH R3592. A. Left lateral view of mid-dorsal vertebra. B. Left lateral view of posterior dorsal vertebra. C. Anterior view of posterior dorsal vertebra. D. Posterior view of posterior dorsal vertebra. E. Left lateral view of one of the most posterior dorsal vertebrae of smaller individual. Scale bars represent 30 mm.

well defined as the posteroventral lamella recedes. The dorsal pit becomes steadily bigger and deeper, and is often complex. The arch also becomes pierced by foramina along the posterior edge of the base of the transverse process and behind the posteroventral lamella. These posterior foramina become less obvious as the posteroventral lamella recedes. The facets of the anterior and posterior zygapophyses become more horizontally inclined. The neural spines are long narrow blades with narrow 'spine tables'.

In an isolated, possibly last, dorsal vertebra (Fig. 24E) from the smaller-sized material belonging to BMNH R3592, the anterior neural arch pits are absent, but the dorsal and posterior ones are highly reduced—only the ventral pits remain well defined. Additional pits are positioned near the proximal end of the facets of the posterior zygapophyses. These neural arch pits are similar to those that can be seen in a wide range of archosaurs, including, for example, rauisuchians (personal observation). They are possibly pneumatic (see Gower 2001), although pneumatized vertebrae are considered at present to be restricted to ornithodiran archosaurs (Britt 1994). *Erythrosuchus africanus* certainly lacks the large pneumatic foramina in the centra of some ornithodiran archosaurs (e.g. Britt *et al.* 1998).

An almost complete and articulated example of the sacral vertebrae and ribs is preserved as part of BMNH R3592 (Fig. 25). *Erythrosuchus africanus* has two sacral vertebrae, the first of which is distinctly larger than the second. The first sacral centrum is circular in end view and is taller than it is long. The anterior edge is ventrally bevelled, probably for articulation with an intercentrum. An intercentrum is preserved in position between the two sacral vertebrae of BMNH R3592. The second sacral vertebra is similar to the first, with a few notable differences. It is smaller and the centrum has an oval-shaped posterior articulatory surface. The facet for the second sacral rib occupies a more posterior position. The possibly pneumatic pits characteristic of the neural arches of the preceding dorsals are absent or greatly reduced on the sacral vertebrae, except perhaps for an excavation behind the process that bears the facet for the first sacral rib.

The caudal vertebrae are well represented by a largely complete and articulated series belonging to BMNH R3592, described only briefly by Huene (1911). There are some glued breakages that may not all be true, but the first 31 caudal vertebrae are well represented. There are at least a further three (and an estimated maximum of five) associated vertebrae. This, together with the fact that at least one vertebra is missing from the tip of the tail, means that the total number of caudal vertebrae was approximately 35. Other specimens include only unassociated examples or fragments, so that possible variations in form and number cannot be assessed currently.

There are a number of changes in morphology along the tail, with the dimensions of some of these variables in BMNH R3592 shown in Table 2. The first caudal vertebra (Fig. 26) is short and high, much like the second sacral vertebra. The single articulatory area for the fused caudal rib is large. The second caudal vertebra (Fig. 26D) is smaller than, but similar to the first. Bevelling of the ventral part of the centrum suggests the presence of an intercentrum in life. Huene (1911) considered the first two caudal vertebrae to be 'caudo-sacral'—believing that the ribs would have contacted the medial surface of the ilium. Although the available evidence (abrupt tapering of the preserved part of the ribs, absence of articulatory areas on the ilium) does not support this view, it is true that the first two caudal vertebrae are laterally flanked by the posterior part of the iliac blade.

TABLE 2

Variation in dimensions of caudal vertebrae in *Erythrosuchus africanus*, specimen BMNH R3592. The dimensions a–i are defined in Figure 19.

Position	Dimensions (mm)						
	a	b	c	d	e	h	i
1	63	87	71	86	70	76	50
2	62	78	67	76		80	
3				68	64		
4	58		72		71		
5	55	68	66		67		
6	54	67	67		64		
7	53	66	63		61	77	50
8	54	61	60		58	75	48
9	53	57	53		52	75	43
10	52	53	49		49	72	45
11	51	50	47		46	72	43
12	49	48	43		43	70	36
13	48	45	42		42	69	35
14	48		38		39	69	34
15	48		38		38	69	
16	47	38	35		36	65	30
17	46		35		34	65	29
18	44	35	34		35	61	28
19	44		34		31	58	27
20	43		30	33	31		26
21	42	32	30	34	32	53	26
22	40	33	30	31	30	53	25
23	39	31	29	28	28	47	23
24	39	30	28	28	26		22
25				29	26		
26	38		27		26	50	
27	37		26		26	49	19
28	35		24		24	46	19
29	34		23	26	23		
30					21		
31			20		19		
32	30		18	19	18		
33		19	17				
34?	23		14	16	13	35	

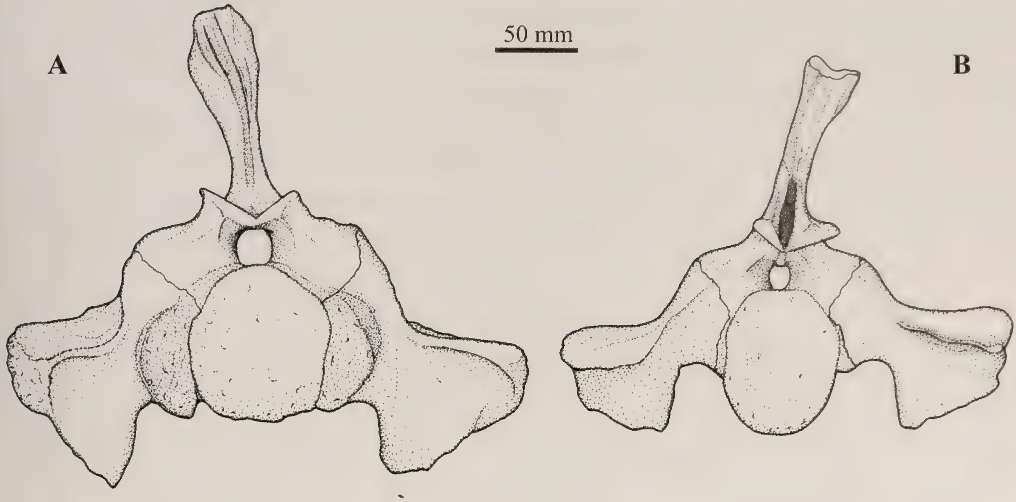

Figure 25

Erythrosuchus africanus, sacral vertebrae and ribs of BMNH R3592. A. Anterior view. B. Posterior view.

Several changes occur over the following eight or so caudal vertebrae (Fig. 27A, Table 2). There is a proportional lengthening of the centra up to a point where the centrum of the tenth caudal vertebra is longer than it is high. This is accompanied by a decrease in the absolute length and diameter of the centra. There is also a reduction in the expression of lateral constriction. The ventral edge remains arched, but the keel is reduced, and the ventral surface becomes a broad and almost flat area. The bevelling on the posteroventral edge of the centra becomes kidney-shaped for articulation with haemal arches. The contact areas for ribs decrease in size, and are positioned lower down on the vertebrae. The articulatory surfaces of the zygapophyses become longer and narrower, and are at a greater angle to one another (the anterior zygapophysial facets of the ninth caudal vertebra are separated by an angle of 125°). The base of the neural spine becomes shorter and is positioned further posteriorly. This change occurs fairly abruptly at the eighth and ninth caudal vertebrae. The complete neural spine of the eleventh caudal vertebra is fairly short and laterally compressed, but has a moderately expanded distal surface. It projects posterodorsally at an angle of approximately 45° to the long axis of the centrum.

The relative lengthening of the centra and reduction in the size of the rib contact areas continues along the remainder of the tail (Fig. 27, Table 2). By the twenty-fourth caudal vertebra the neural spine is but a low, thin crest. Posterior to the twenty-fourth caudal and up to the end of the tail, the angle between opposite zygapophyseal surfaces again narrows—to a point where they are almost vertical, and significant lateral movement of the tail would have been greatly restricted. In a horizontal plane the tail would have been stiff at its base and again towards the tip, with more potential for movement between these points. By the twenty-ninth caudal vertebra there is no longer a contact area for a caudal rib, and by the thirty-second the neural spine is reduced to a barely perceptible ridge.

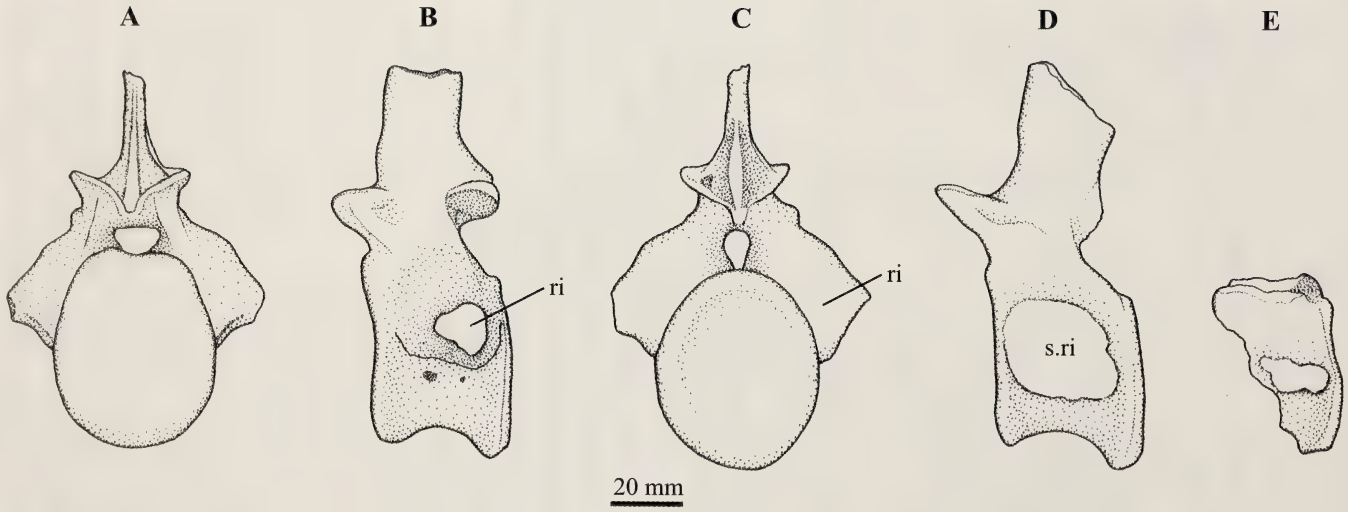

Figure 26

Erythrosuchus africanus, anterior caudal vertebrae of BMNH R3592. A. Anterior view of first caudal vertebra. B. Left lateral view of first caudal vertebra. C. Posterior view of first caudal vertebra. D. Left lateral view of second caudal vertebra. E. Left lateral view of third caudal vertebra.

The presacral ribs are poorly known. BMNH R3592 includes one fairly complete cervical rib (Fig. 28A) and some additional fragments. The shaft of the cervical rib is short, laterally compressed but slightly concavo-convex, and tapers to a point. The capitulum and tuberculum are short, and their facets lie close together. The tubercular facet is circular but the capitular one is more oval in shape. A small leaf-shaped and laterally compressed anterior process of the shaft projects forward between the capitulum and tuberculum. Grooves, possibly for blood vessels, are located on the ventro- and dorsomedial edges, just behind the base of the tuberculum and capitulum. The other known fragments of cervical ribs show no notable deviation from this morphology.

The pectoral ribs of early archosaurs are of particular interest because of a number of claims and refutations of the presence of three-headed ribs (Huene 1960; Tatarinov 1961; Hughes 1963; Ewer 1965; Charig & Reig 1970; Cruickshank 1972; Thulborn 1979; Peng 1991; Parrish 1992). Excepting Tatarinov (1961), it has generally been accepted that three-headed ribs were not present in *Erythrosuchus africanus*. Most recently, Parrish (1992) has claimed that three-headed ribs are present only in the pectoral region of *Vjushkovia triplicostata* Huene, 1960, and *V. sinensis* Young, 1973, and that they are a synapomorphy of the genus *Vjushkovia*. Evidence from a pectoral vertebra belonging to BMNH R3592 described above, suggests however that they were present in *Erythrosuchus africanus*. An incomplete rib belonging to SAM–3028 (Fig. 28B) offers further support for this interpretation. It is an almost complete proximal end with a short fragment of shaft. There is no anterior process, the capitular and tubercular 'peduncles' are confluent with the proximal end of the shaft, and the articulatory facets are oriented virtually perpendicular to the long axis of the shaft. The ventral margin is arched but the dorsal one is nearly straight.

The capitular facet is oval-shaped and simple. The tubercular facet is slightly larger and more circular, and closely associated with its ventral edge is a small but discrete accessory facet. The posterior view of this rib shows that this third facet is not just an expanded area of a lamella between the capitular and tubercular facets, but that it is associated with its own cylindrical peduncle. This arrangement is very similar to the pectoral ribs of *Vjushkovia triplicostata* (Huene 1960; personal observation). This rib morphology, combined with the above description of the pectoral vertebra of BMNH R3592 with three apophyses, provides the first detailed osteological evidence that three-headed ribs were present in *Erythrosuchus africanus*. The presence of three-headed pectoral ribs is not therefore a unique synapomorphy of the genus *Vjushkovia* (see also Gower & Sennikov 2000).

The evidence from the apophyses of the anterior dorsal vertebrae is that the anterior dorsal ribs were dichocephalous. Substantial shaft fragments and a possible distal end of a large dorsal rib belong to BMNH R3592, but no proximal ends are known. Posterior dorsal ribs (e.g. Fig. 28C) are known only from proximal fragments.

The sacral ribs (Fig. 25) are short, stout, and ventrolaterally directed. They are very firmly attached to the sacral vertebrae, but a suture is still evident. The ribs of the first sacral vertebra are much larger than those of the second. Anteromedially they protrude beyond the anterior surface of the centrum to provide additional articulatory surfaces for

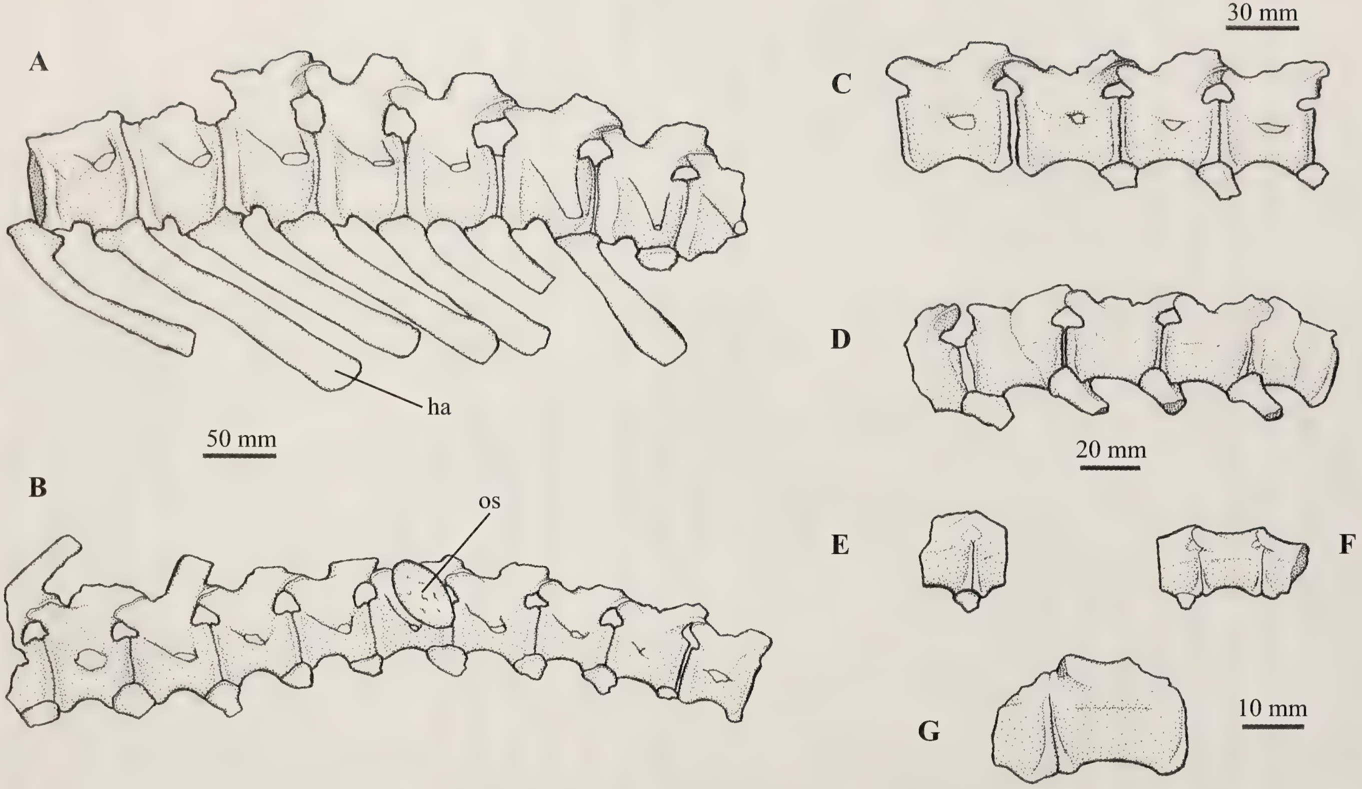

Figure 27

Erythrosuchus africanus, left lateral views of caudal vertebrae of BMNH R3592. A. Fourth to eleventh caudal vertebrae. B. Eleventh to twentieth caudal vertebrae. C. Twenty-first to twenty-fourth caudal vertebrae. D. Twenty-fifth to twenty-ninth caudal vertebrae. E. Thirtieth and thirty-first caudal vertebrae. F. Thirty-first to thirty-third caudal vertebrae. G. Thirty-third and thirty-fourth caudal vertebrae.

the centrum of the last dorsal vertebra. The second sacral ribs articulate with the more posterior part of the vertebra, and do not extend beyond the posterior edge of the centrum.

All of the caudal ribs (Figs 26, 27) are holocephalous and are firmly attached to the vertebrae, although a suture can often be detected. The ribs of the first two caudal vertebrae have very robust heads, but the short shaft tapers distally. The remaining ribs are all dorsoventrally flattened, short, and project downwards and slightly posteriorly. They become shorter and more slender along the length of the tail, before disappearing by about the twenty-ninth caudal vertebra.

Intercentra and haemal arches

The presence or absence of intercentra has been employed as a character that has importance for the resolution of early archosaur relationships (e.g. Benton & Clark 1988; Sereno 1991; Parrish 1992). Despite some debate over the presence of intercentra in erythrosuchids (e.g. Charig & Reig 1970) it is clear that intercentra were present throughout the precaudal column in *Erythrosuchus africanus*. This is partly demonstrated by the obvious bevelling on the anterior and posterior ventral edges of the centra. Contrary to Parrish (1992), intercentra are preserved in some specimens of *E. africanus*. One is preserved in BPI 4680 (Fig. 28F), and three articulated dorsal vertebrae from SAM–PK–K10025 show intercentra preserved in articulation (Fig. 28E). An intercentrum is also present between the two sacral vertebrae of BMNH R3592. The first two caudal vertebrae of BMNH R3592 show bevelling, yet not the expanded kidney-shaped area of the more posterior caudals. This suggests that intercentra but not haemal arches were present here. The anterior edge of the third caudal centrum is not preserved, but between the third and fourth and all subsequent caudals there are haemal arches, but no sign of separate intercentra. This is different from the condition in *Proterosuchus*, where separate caudal haemal arches and intercentra are present (Cruickshank 1972).

Haemal arches (Fig. 28D), or chevrons, are present from between at least the third and fourth caudal vertebrae up to the end of the tail. They all share the same general structure in possessing a broad, hour-glass or kidney-shaped proximal end, and a posteroventral Y-shaped distal process. They articulate largely with the broad area on the posteroventral bevelled edge of each caudal centrum, although contact with the anteroventral edge of the following centrum is also achieved. The anteriormost haemal arches have long and almost cylindrical distal ends, but several changes in form occur along the tail. They become shorter more abruptly than the decrease in length of the corresponding centra, and the openings for the passage of the blood vessels of the tail become smaller. The distal ends gradually become laterally compressed, and they also develop a projecting, lamella-like anterior edge. The lateral compression is combined with a small degree of torsion, so that the right side of each haemal arch is rotated anteriorly and the left side posteriorly. There is direct evidence of haemal arches being present at the thirty-second caudal vertebra, and further indirect evidence (in the broad bevelling of centra) that they were present beyond this and possibly up to the tip of the tail.

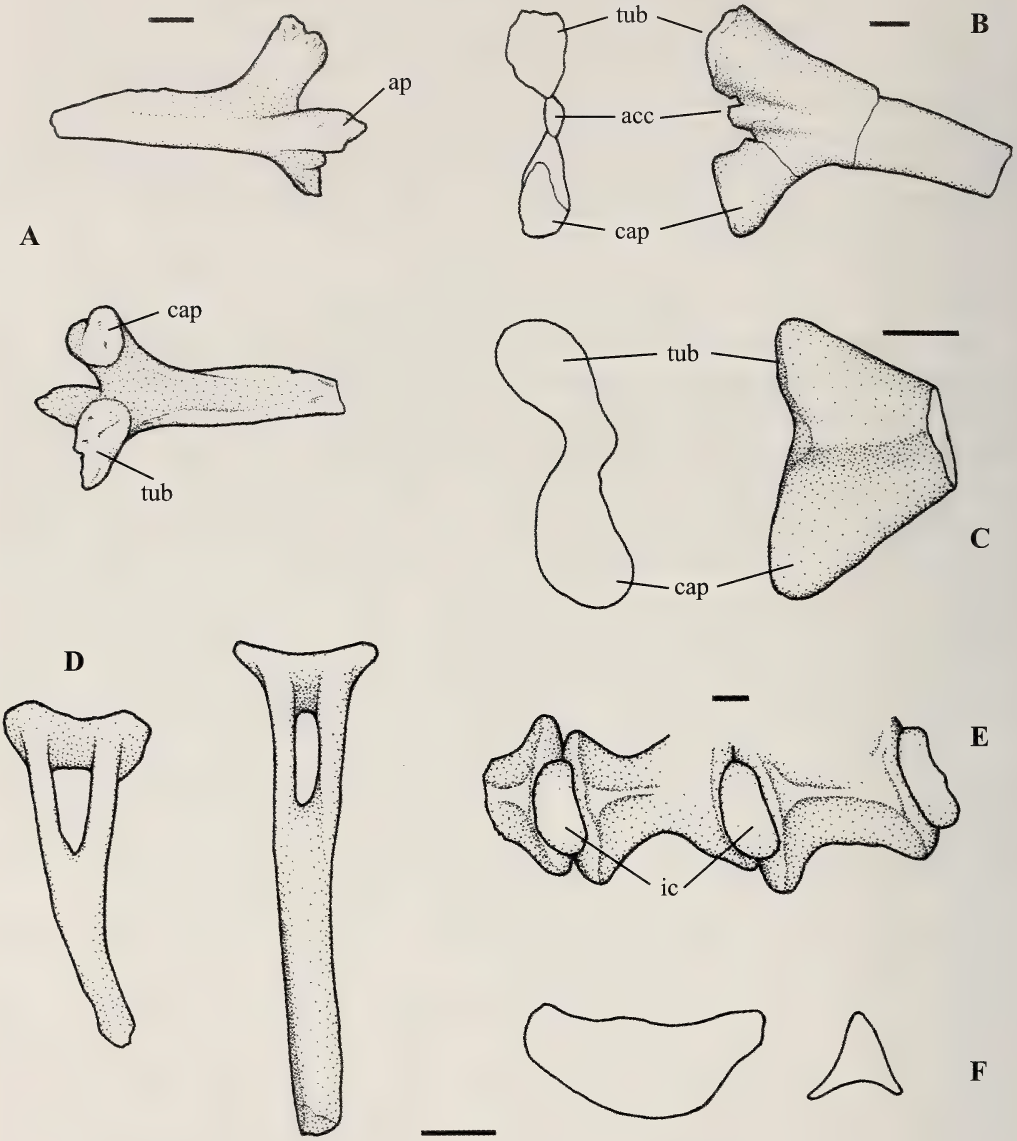

Figure 28

Erythrosuchus africanus. A. Lateral and medial views of anterior right cervical rib of BMNH R3592. B. Medial and anterolateral views of left pectoral rib of SAM–3028. C. Medial and anterolateral views of left posterodorsal rib of BMNH R3592. D. Anterior views of the anteriormost and a slightly more posterior haemal arch of BMNH R3592. E. Ventral view of dorsal centra and intercentra of SAM–PK–K10025. F. Anterior and lateral outlines of isolated intercentrum of BPI 4680. All scale bars represent 15 mm.

APPENDICULAR ELEMENTS

Limb orientation terminology

The clarity of osteological descriptions and their usefulness in comparative studies is often clouded by the lack of a definition of the terms used to orient limb surfaces. In choosing a set of clearly-defined and practical terms, it is here intended to use those based on form rather than on a postulated and potentially incorrect life position. This avoids the vagaries of discrete gaits, that are usually too rigid and generalized (e.g. Jenkins 1971). The terminology used here is based on the early ('primitive') tetrapod condition, rather than that used in dinosaurian, avian, and mammalian studies—groups generally considered to have an 'upright' gait. This terminology therefore aims to agree with that already established in the osteological and myological description of extant quadrupedal archosaurs (for example, that applied to crocodilians by Romer 1942), despite the additional problems caused by differences in the relative position of homologous surfaces on single elements among different taxa. Romer (1922, 1923, 1942) defined the dorsal and ventral surfaces for the propodial elements of the fore- and hindlimb of early tetrapods. The ventral surface of the 'primitive' tetrapod humerus, as described by Romer, is broadly equivalent to the anterior surface of the dinosaurian (or mammalian) humerus, but the ventral surface of the 'primitive' tetrapod femur is equivalent to the posterior of the dinosaurian femur. This difference is a result of the flexural differences between the fore- (at the elbow and wrist) and hind- (knee and ankle) limb. This disagreement represents a fundamental problem in attempting to employ a consistent terminology for limb orientation.

In the works cited above, Romer was not concerned with the epipodials or the carpal/tarsal elements. Rewcastle (1980) approached this problem, with respect to the hindlimb of extant lizards, by standardizing a terminology to a fully, anteriorly extended limb. Rewcastle's study concerned the hindlimb only, and did not have to confront the problems concerned with translating this same reasoning to the forelimb.

Although the differences in flexure mean that some disagreement must remain between the fore- and hindlimb terminology, the main objective is to be explicit about the terminology used. With respect to the hindlimb, I follow Rewcastle's (1980; see also Gower 1996) terminology, but with the forelimb I attempt to apply some of Rewcastle's reasoning as well as following Romer's traditional definition of dorsal and ventral. Thus the long axes of all the limb bones are parallel to the long axis of the body in lateral view. The 'standard' posture of the forelimb is with the radius, ulna, carpus, and manus fully anteriorly extended, but the humerus fully posteriorly extended. The dorsal and ventral surfaces of the epipodials and manus/pes can, of course, be termed extensor and flexor surfaces respectively. Although explicit in its definition, it is realized that this terminology is far from perfect, and that a 'standard' posture is 'somewhat arbitrary' anyway (Rewcastle 1980).

Pectoral girdle and limb

The only elements of the pectoral girdle of *Erythrosuchus africanus* that are currently known are the scapula and coracoid. The slightly incomplete scapula of the type

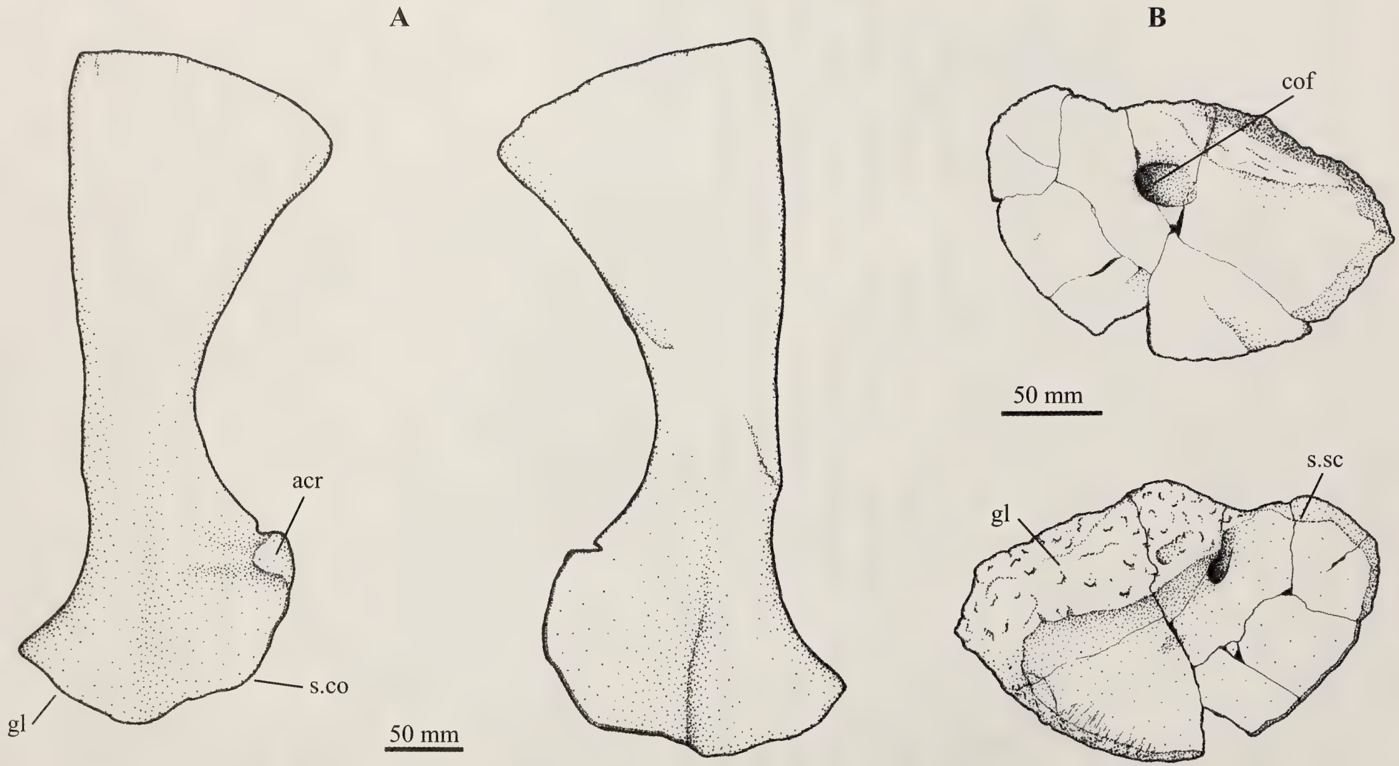

Figure 29

Erythrosuchus africanus, pectoral girdle. A. Lateral and medial views of right scapula of BMNH R3762a. B. Lateral and medial views of left coracoid of BMNH R3592.

specimen, SAM–905, was briefly described by Broom (1906). Only worn fragments are preserved as part of BMNH R3592 (not described by Huene 1911), and there are two incomplete and crushed examples preserved as part of SAM–3028. The best specimen is a well-preserved and complete right-side example—BMNH R3762a (Fig. 29A)—that is shorter and more slender than that of the holotype.

The scapula (Fig. 29A) is tall, fairly slender, and much larger than the coracoid. The long axis of the element is bowed so that the lateral surface is convex and the medial surface concave. The anterior margin, when viewed laterally, is concave, whereas the posterodorsal margin is neither strongly posteriorly directed nor tapering. The overall outline of the scapula therefore resembles that of later archosaurs, and is the converse of that seen in archosauromorphs more distant from the crown, such as *Proterosuchus* (Cruickshank 1972) and *Prolacerta broomi* (Gow 1975).

The anterior margin of the scapula blade is thin, apart from a prominent anterolateral process at the distal end. This might be termed the acromion process although there is no direct evidence that its function was the support of a clavicle. Close to where the scapula narrows to a 'waist', the posterior edge of the medial surface bears a thin, vertical ridge—possibly associated with the origin of the *m. subcoracoscapularis*. A low ridge positioned slightly distal to this, and close to the anterior margin, borders a shallow depression that opens out on to the dramatically expanded distal end of the scapula.

The coracoid (Fig. 29B) is a remarkably small element compared with the scapula. The anterior of the coracoid is thin and plate-like, but the posterior edges, particularly dorsally, are greatly thickened—up to 4.5 times as thick as the anterior edge in BMNH R3592. These edges are also highly rugose. The dorsally expanded area represents the ventral surface of the glenoid fossa, which is quite different from that of *Proterosuchus* (Cruickshank 1972) in being an essentially simple and posteriorly open notch—although the socket in life may have been shaped largely by cartilage. The foramen for the passage of the supracoracoid nerve is entirely within the coracoid.

The humerus (Fig. 30) is a short robust bone. The strongly expanded proximal and distal ends are joined by a short, cylindrical shaft. The angle between the long axes of the two end surfaces is approximately 30° in SAM–905.

The ventral surface of the proximal end is dominated by a large deltopectoral crest. In the largest specimens (SAM–905, BMNH R3592), the crest is almost rectangular in lateral view and extends to almost halfway down the shaft. In smaller specimens (BMNH R3762, SAM–PK–K10025), the crest is a less angular and less prominent feature, and the shaft is more slender. In BMNH R3592, a rugosity on the lateral surface of the base of the deltopectoral crest is interpreted as part of the area of insertion of the deltoid musculature.

The slightly concave and rugose surface of the distal end suggests that the capitellum and trochlea were largely cartilaginous features in life. The supinator process is well developed and its ventrolateral edge continues up on to the base of the deltopectoral crest as a low supinator ridge. The dorsal edge of the supinator process forms the ventral border of a deep ectepicondylar groove for the radial nerve and blood vessels.

The radius (Fig. 31A) of *Erythrosuchus africanus* is known only from a single, complete example from the right side of SAM–905. The area of the proximal surface is

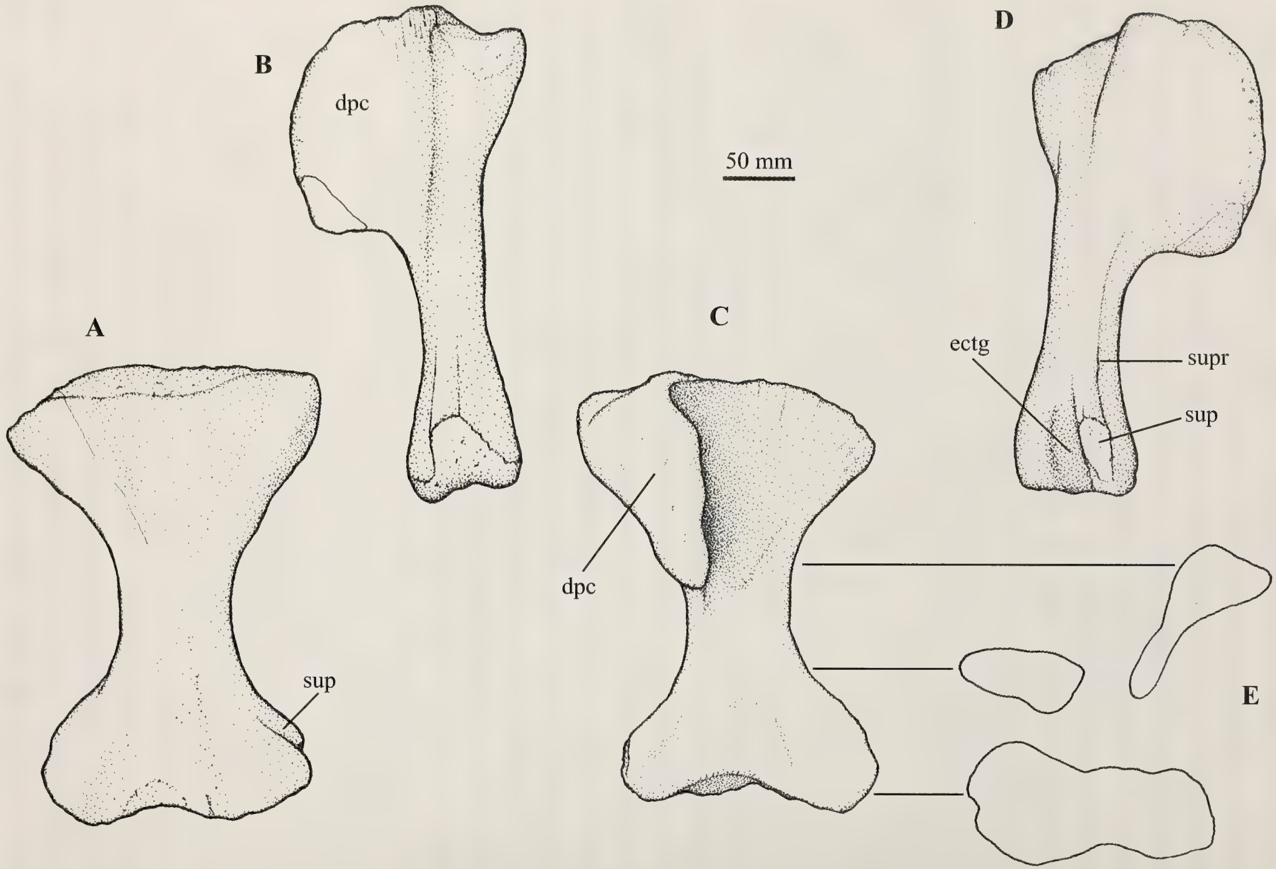

Figure 30

Erythrosuchus africanus. A. Dorsal view of right humerus of SAM–905. B. Medial view of right humerus of SAM–905. C. Ventral view of right humerus of SAM–905. D. Lateral view of right humerus of SAM–905. E. Proximal views of transverse outlines of right humerus of BMNH R3592, not to same scale.

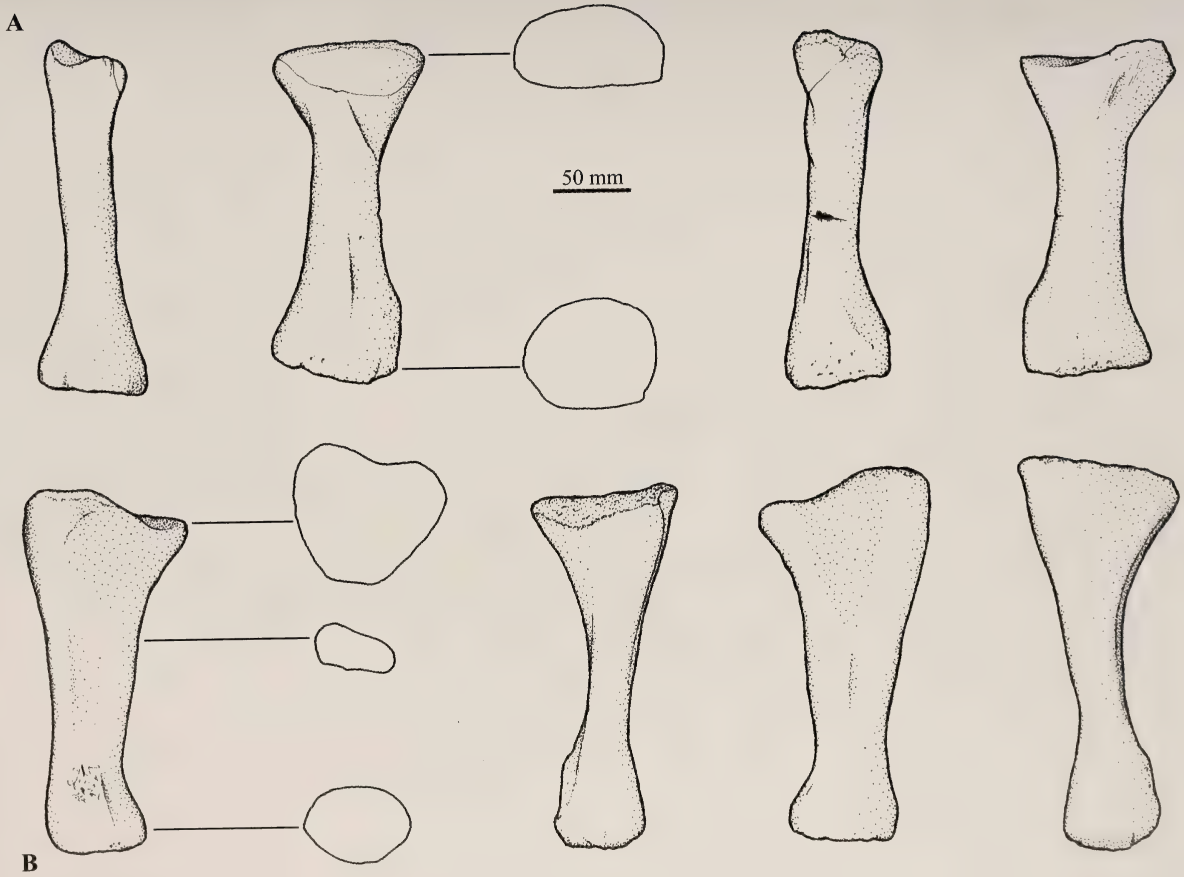

Figure 31

Erythrosuchus africanus, forelimb epipodials of SAM–905. A. Right radius in lateral, dorsal, transverse, medial, and ventral views. B. Right ulna in lateral, transverse, dorsal, medial, and ventral views. Transverse outlines are proximal views.

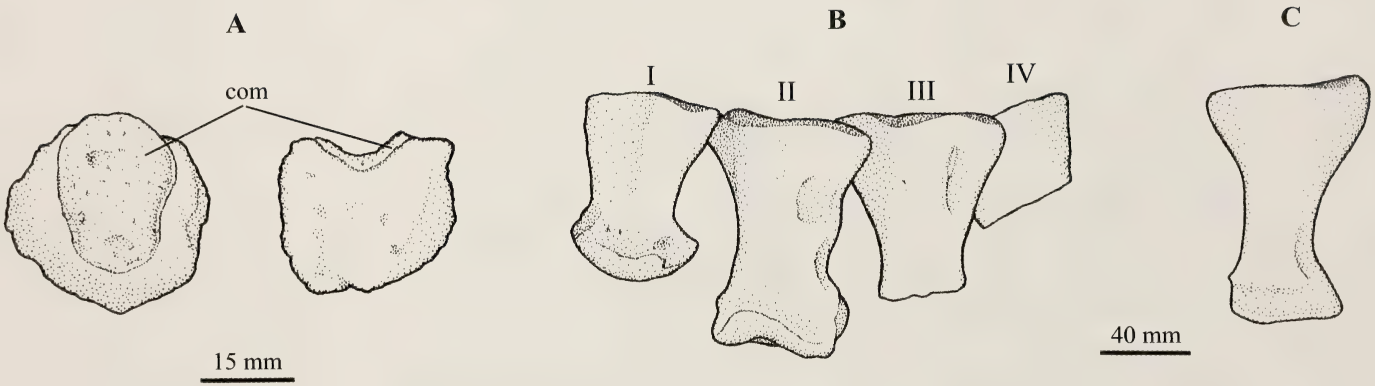

Figure 32

Erythrosuchus africanus. A. Possible carpal of BMNH R3592 in two views. B. Dorsal view of first four left metacarpals. C. Dorsal view of right fourth metacarpal of BMNH R3592.

much smaller, and the distal end larger, than the corresponding ends of the ulna. The dorsal surface bears two clear ridges, possibly representing areas of muscle attachment.

The ulna (Fig. 31B) is slightly longer and more heavily built than the radius. As with the radius, the only complete example is from the right forelimb of SAM–905. The proximal articular surface is terminal and there is no ossified olecranon process above it. The surface is rugose, concave, and sub-triangular in shape. The shaft is essentially oval in cross-section and apart from a low medial ridge, and a less prominent lateral ridge, it is relatively featureless. The lateral surface of the distal end is roughened and slightly raised.

The carpus and manus of *Erythrosuchus africanus*, as in many early archosaurs, is very poorly known. A small spherical bone not belonging to the tarsus is among the material belonging to BMNH R3592 (Fig. 32A). Its surface is poorly ossified apart from a saddle-shaped area of roughened compacta. It is here tentatively identified as a carpal element.

As with the carpus, the only information on the rest of the manus of *Erythrosuchus africanus* comes from BMNH R3592. There are elements of what are probably two individuals of clearly different sizes. These probably correspond to the two individuals represented by the two different size categories of vertebral material catalogued under the same number. Belonging to the larger size category, and probably belonging to the individual represented by the vast majority of specimen BMNH R3592, are the first four left metacarpals (third and fourth incomplete) and the fourth right metacarpal (Fig. 32B, C). Belonging to the smaller individual are the first three left metacarpals (third incomplete), the proximal end of the second left metacarpal, and a single phalanx, probably from the first digit. At least the left carpal material of the larger individual was originally catalogued as part of DMSW R525. All of the metacarpals show torsion along their length and the proximal ends are closely overlapping. Of the four metacarpals known, the first is the shortest followed by the second, with the third being marginally shorter than the fourth. Nothing is known of either the fifth metacarpal or of the phalangeal formula. The larger metacarpals, particularly the proximal surfaces, are similar in size to the metatarsals of the same specimen.

Pelvic girdle and limb

The pelvic girdle (Fig. 33) resembles that of other early archosaurs in having a short pubis and ischium, and a closed acetabulum. All of the articular surfaces between the girdle elements are rugose. The anterior extension of the crest of the ilium (Fig. 33A) is not strongly developed (and becomes less obvious in larger specimens), but here it is at its thickest, bears heavy dorsal striations, and was probably the area of *m. iliofemoralis* and *m. iliotibialis* attachment. Ventrally, the medial edge of the crest is thickened, and the dorsal edge remains narrow. The downturned sacral ribs and prominent supra-acetabular crest combine to present a ventrolaterally directed acetabular socket.

The medial surface of the ilium bears the large, shallow, and sculptured depression that receives the head of the first sacral rib. The depression for the second sacral rib is smaller and extends for a short distance on to the anteroventral part of the base of the iliac crest. The two depressions, separated by a low, vertical ridge, closely match the lateral surfaces of the two sacral ribs.

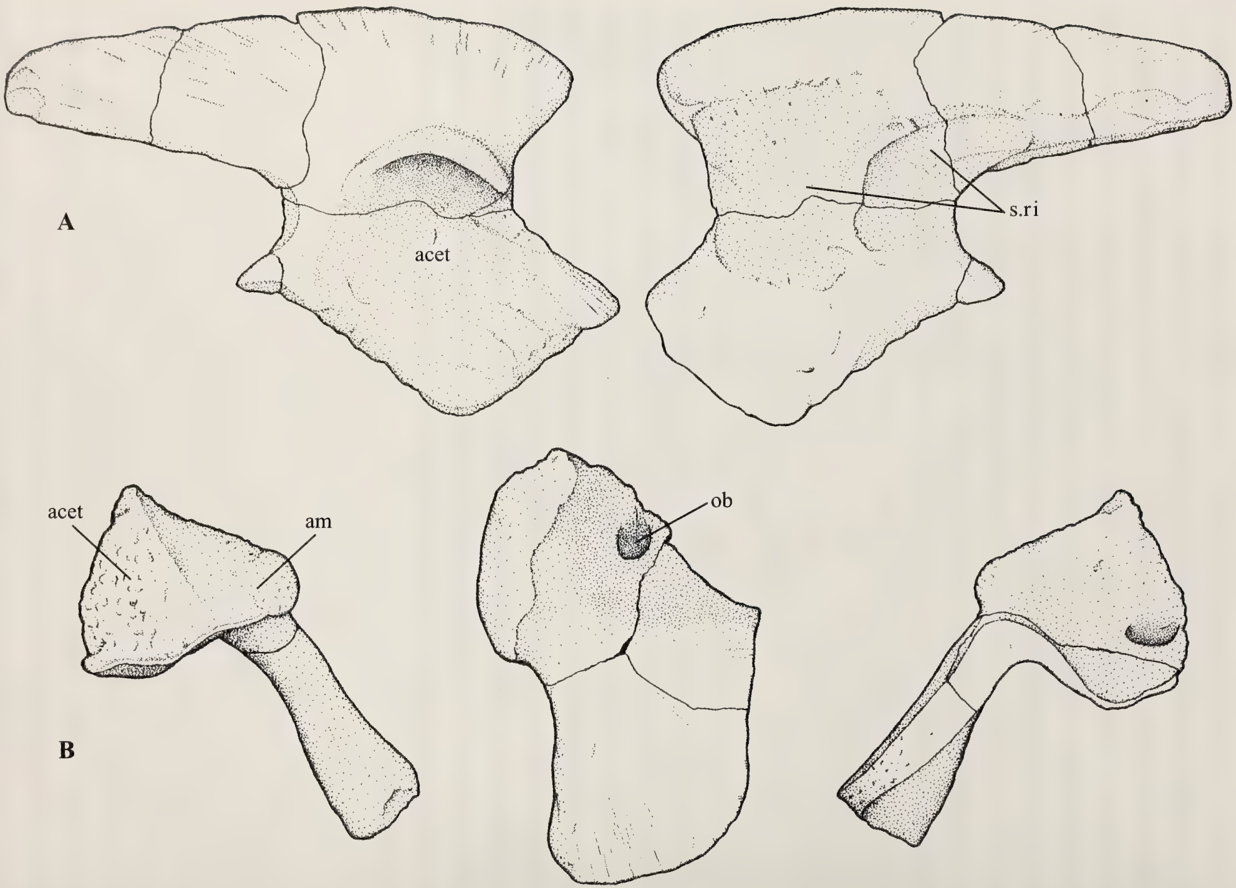

Figure 33A & B

Erythrosuchus africanus, right pelvic girdle elements of BMNH R3592. A. Lateral and medial views of ilium. B. Lateral, anterodorsal, and medial views of pubis.

The pubis (Fig. 33B) forms the rather weak anteroventral border of the acetabulum. The surface for articulation with the ilium is greatly expanded to form a broad, triangular area. This is much larger than the corresponding surface on the ilium and the excess forms a rugose anteroventral acetabular border. The head of the pubis remains roughened and raised in front of the anterior margin of the acetabulum, and this probably represents the site of the *m. ambiens* origin.

The remainder of the pubis is composed of two confluent and flattened plates of bone. One projects medially, in a horizontal plane from the head of the pubis, and the other is oriented almost at a right angle to the first to form the short, downturned part of the pubis. An oval-shaped obturator foramen is positioned close to the posterior edge and just medial to the head of the pubis. The downturned plate has a greatly thickened and cylindrical lateral edge that ends abruptly in a roughened surface.

The anterodorsal part of the ischium (Fig. 33C) is expanded to form the posteroventral border of the acetabulum. The remainder of the element consists of a broad, dorsomedially-ventrolaterally flattened, and slightly ventrally concave plate. A number of ridges towards the posteromedial margin of the dorsal surface of the ischium might have been associated with the origin of the *m. ischiotrochantericus*. The reconstructed angle between the dorsal surfaces of the ischia when articulated is estimated to be approximately 115° anteriorly and 45° posteriorly.

The femur (Fig. 34) of *Erythrosuchus africanus* is considerably longer than the humerus—in BMNH R3592 the ossified part of the femur is approximately 1.25 times as long as the estimated ossified part of the humerus. The proximal and distal articular ends are terminal and their faces are approximately perpendicular to the long axis of the shaft. Both end surfaces are rugose, concave, and bear a central longitudinal groove—suggesting that substantial cartilaginous caps would have formed the finished articulatory surfaces. The proximal and distal ends are slightly up- (dorsally) and down- (ventrally) turned respectively, although to a lesser degree than is seen in, for example, *Prolacerta broomi* (Gow 1975) and proterosuchids (personal observation). The shaft is robust and shows some degree of torsion, with the long axis of the distal articulatory surface offset at an angle of approximately 25° to the long axis of the proximal surface. The femur is not as straight as in *Proterosuchus* (Cruickshank 1972; personal observation) when viewed dorsally or ventrally, with the proximal end clearly deviating from the long axis of the shaft.

On the ventral surface of the proximal end there is a large and well-defined intertrochanteric (adductor) fossa. Bordering this medially, and lying a short distance away from the proximal terminus of the femur, is a prominent flange-like trochanter. This was probably an insertion site for at least part of the caudifemoral musculature, based on comparisons with extant lizards (Snyder 1954; Walker 1977) and crocodilians (Romer 1923; Walker 1977). The proximolateral surface of the trochanter, together with the fossa, are interpreted as a probable insertion site of the *m. puboischiofemoralis externus*. Extending diagonally from the distal end of the trochanter towards the lateral edge of the distal end is a well-defined ridge (adductor crest) for the *m. adductor femoralis*.

The edge of the femur lateral to the intertrochanteric fossa is narrow proximally. It broadens out abruptly at a point level with the distal termination of the intertrochanteric

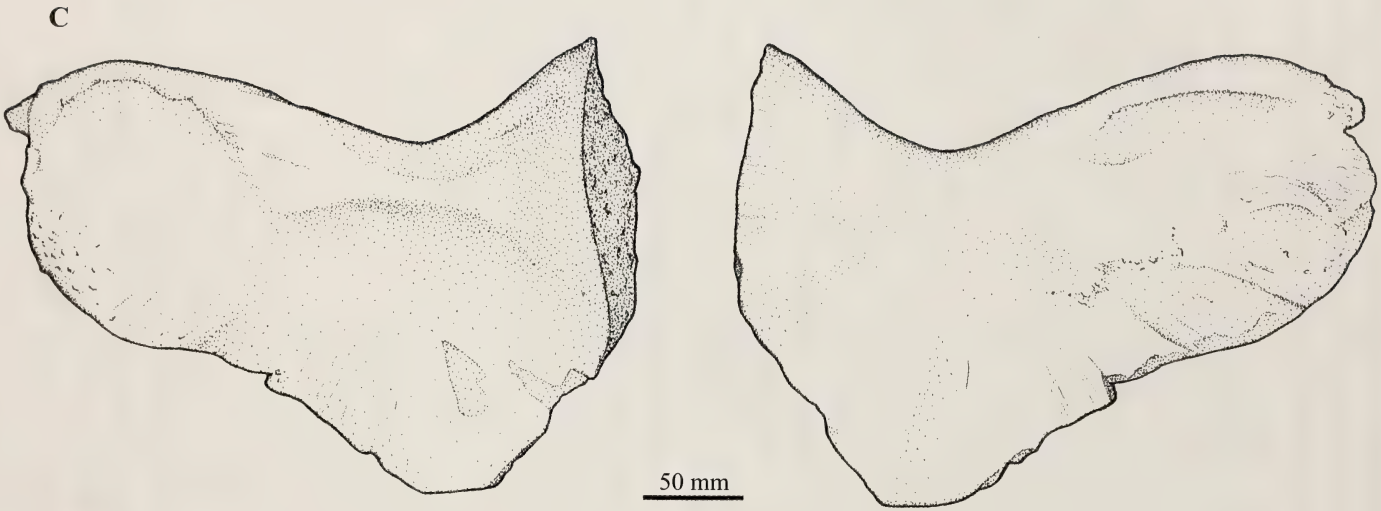

Figure 33C

Erythrosuchus africanus, right pelvic girdle elements of BMNH R3592. C. Ventrolateral and dorsomedial views of ischium.

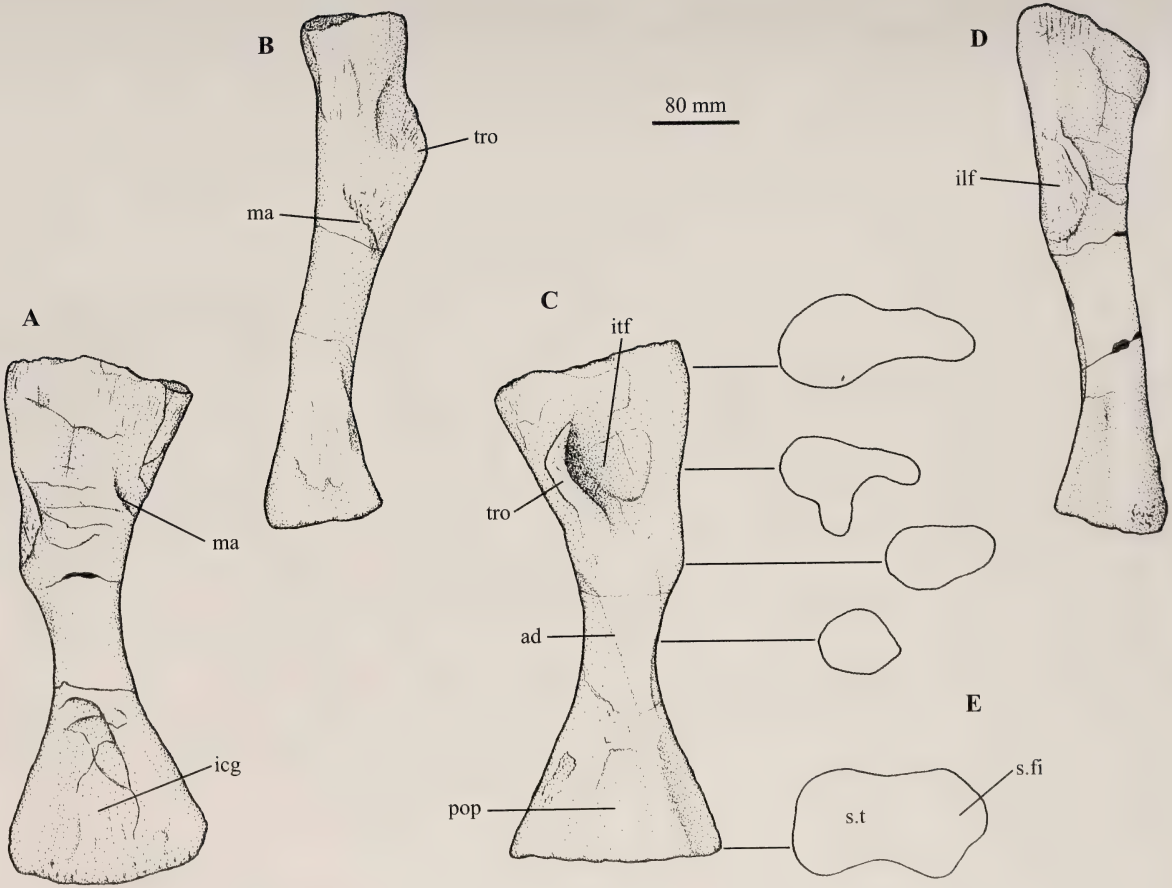

Figure 34

Erythrosuchus africanus, right femur of BMNH R3592. A. Dorsal view. B. Medial view. C. Ventral view. D. Lateral view. E. Transverse outlines in proximal view.

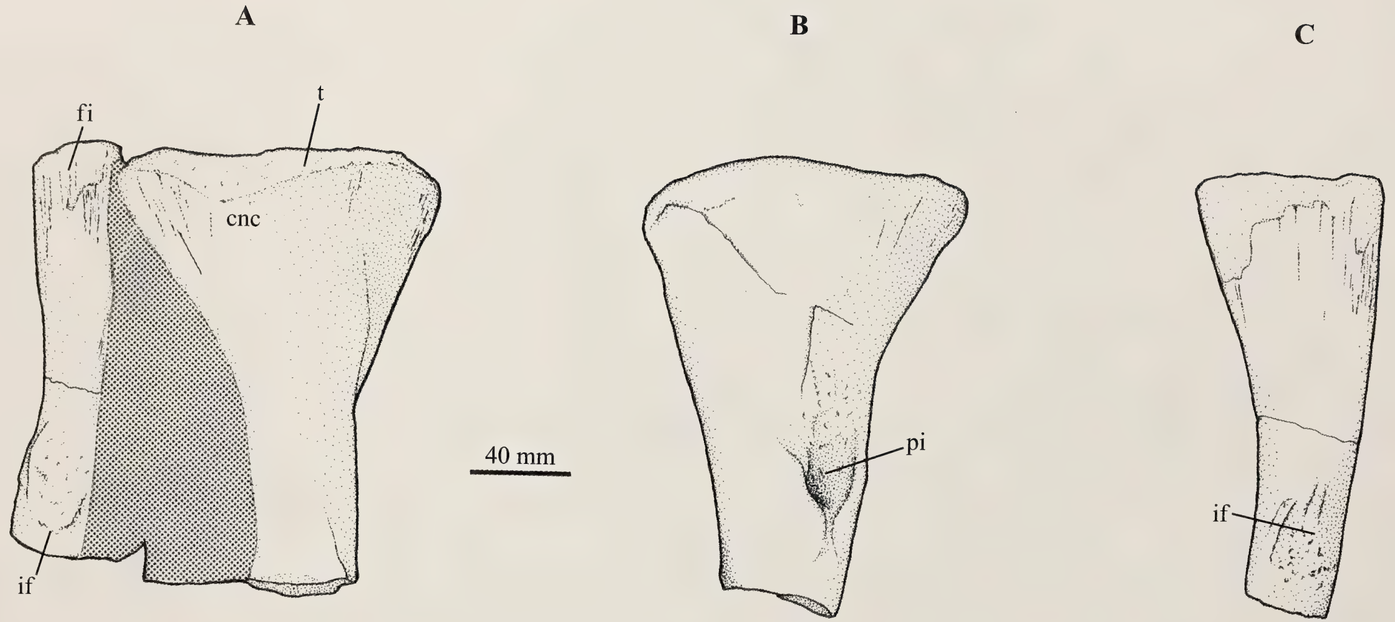

Figure 35A, B & C

Erythrosuchus africanus, crus of BMNH R3592. A. Proximal part of right side in dorsal view. B. Proximal part of right side in medial view. C. Proximal part of right side in lateral view.

fossa, and forms an oval-shaped, dorsolateral swelling that extends distally to a point just beyond one-third down the length of the shaft. This was identified as the trochanter major by Gregory & Camp (1918, fig. 11), but Parrish (1992, fig. 2) considered it to be a fourth trochanter. When the various trochanters are considered in terms of probable muscle attachment sites, the identification of this as a fourth trochanter seems extremely doubtful. The fourth trochanter of more derived archosaurs is a ventral feature positioned a significant distance from the proximal end and, like at least part of the internal trochanter of non-archosaurian diapsids, is a site for the insertion of caudifemoral musculature. Whatever the name applied to this prominence, it seems a much more satisfactory interpretation that this area, in *Erythrosuchus africanus*, was for the attachment of the *m. iliofemoralis* and not the *m. caudifemoralis*, particularly when one considers the actions that these muscles perform.

The ventral surface of the distal end of the femur is dominated by a large popliteal space that, together with a wide groove on the ventrolateral edge, extends about one-quarter of the way up the femoral shaft. The dorsal surface of the femur is less contoured (Fig. 34A). The dorsal part of the trochanter for the *m. iliofemoralis* can be seen on the proximoposterior edge, and just proximal to this is a further scar that perhaps is the insertion site of the *m. ischiotrochantericus*. Distally, there is a shallow and broad intercondylar groove for the extensor tendon of the *m. quadriceps femoris*.

No complete tibia (Fig. 35) is known, but knowledge has been gathered from various incomplete specimens representing proximal (BMNH R3592, left and right) and distal (BMNH R3592, left and BPI 2096, right) ends. Huene (1911) interpreted the proximal sections of the right tibia and fibula of BMNH R3592 (Fig. 35A–C) as distal ends. The tibia is considerably shorter than the femur—an estimated 72 per cent of the length of the femur in BMNH R3592. Approximately one-third down the length of the tibia the shaft is cylindrical and at its narrowest. At this point and on the medial edge, there is a deep and well-defined pit that is interpreted as a likely area for the insertion of the *m. puboischiotibialis*.

The shaft remains cylindrical and straight for the middle third of the tibia. At this midpoint, at least, the shaft of the tibia is like that of the other limb bones for which clean broken sections are available, in that it has a hollow core surrounded by a thin region of cancellous bone. The gradual distal expansion of the tibia curves laterally towards the fibula. A roughened area of bone and an adjacent low ridge on the dorsolateral surface of the distal end might be the attachment site of a muscle lying between the hindlimb epipodials. There is a similar, but more diffuse scar on the medial edge of the tibia. The distal end of the tibia is almost circular in shape, and the surface is concave and weakly ossified (Cruickshank 1978). Examination of the lateral surface of the distal end of the tibia of BMNH R3592 supports Cruickshank's (1978) suggestion that the 'lateral process' present in BPI 2096 is an artefact of preservation.

As with the tibia, there is no complete fibula (Fig. 35) currently known for *Erythrosuchus africanus*. However, examination of various incomplete examples allows a description of the whole element to be presented. These are BMNH R3592 (right proximal), BMNH R3592 (formerly DMSW R525, left distal), and BPI 2096 (right distal). In all cases these fibulae are clearly associated with the corresponding tibiae.

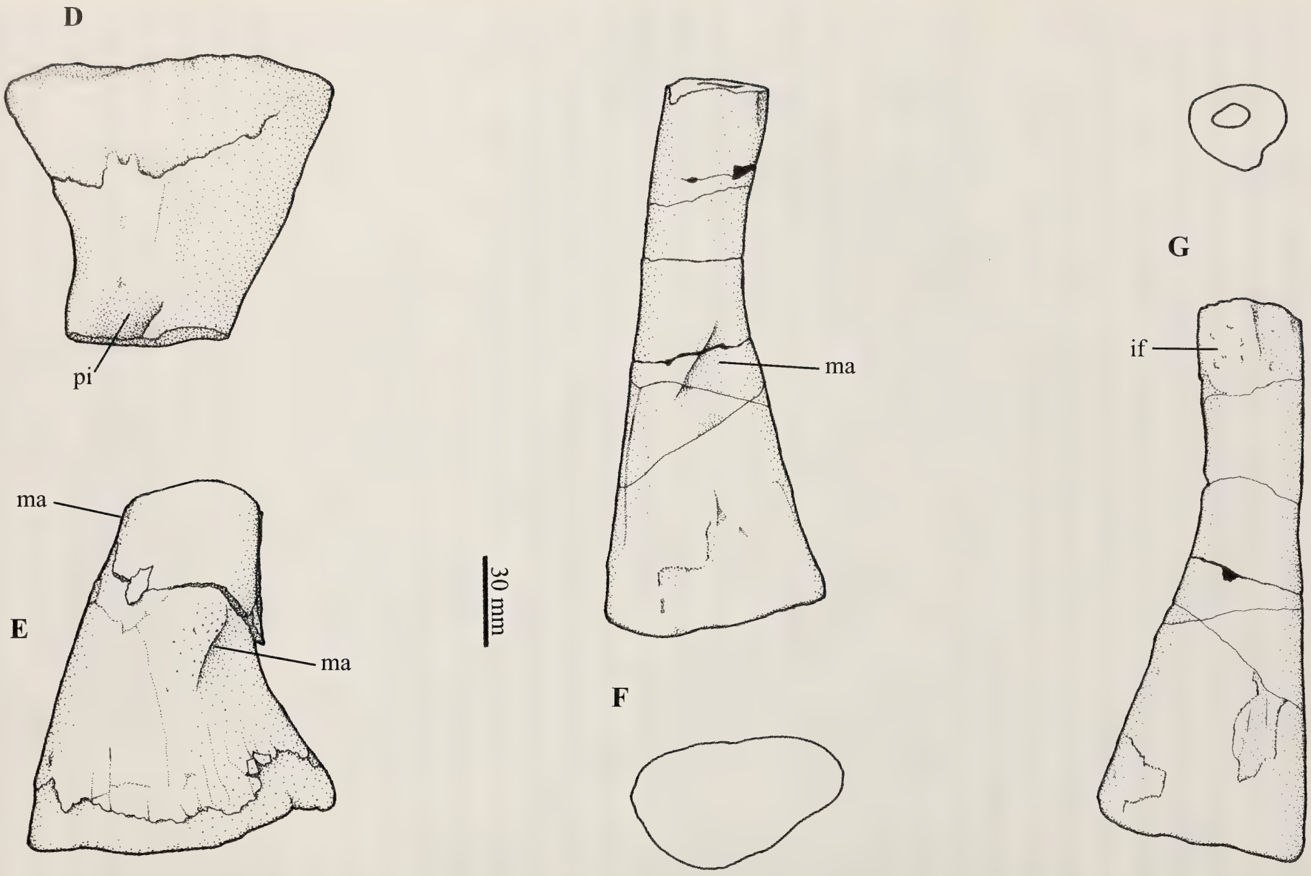

Figure 35D, E, F & G

Erythrosuchus africanus, crus of BMNH R3592. D. Proximal part of left tibia in medial view. E. Distal part of left tibia in dorsal view. F. Ventral and distal views of distal part of left fibula. G. Dorsal and proximal views of distal part of left fibula. Upper scale bar accompanies A to D; lower scale bar accompanies E to G.

The fibula is much more slender than the tibia, and the long axes of the proximal and distal ends are approximately perpendicular to one another. The proximal limit of a roughened and prominent scar for the *m. iliofibularis* is positioned about one-third of the distance along the dorsolateral edge. This scar extends distally to a point just below half-way down the shaft—by which point it has shifted to a dorsal position. A low but well-defined ridge, distal to the *m. iliofibularis* scar and on the medial edge of the fibula, is here interpreted as the possible fibular point of attachment of a muscle situated between the fibula and tibia, possibly the *m. interosseous cruris*. An additional muscle scar forms an unroughened, step-like ridge on the ventral surface of the fibula. The distal end surface is oval in shape, gently concave, and covered in only a very thin veneer of compact bone (as was possibly the proximal end before preservation/preparation). It is a little larger in area than the proximal end.

The tarsus and pes have been described, at least in part, by Huene (1915, 1920), Hughes (1963), Cruickshank (1978), and Brinkman (1981). Parrish (1992: 100) questioned the referral of the tarsal material to *Erythrosuchus*, but Gower (1996) supported the original identifications and presented a detailed redescription of the known material.

GASTRALIA

The gastralia are poorly known but some examples are represented in three small blocks of matrix belonging to BMNH R3592. These gastralia were not described by Huene (1911), but are here interpreted as belonging to *Erythrosuchus africanus*. The best of these examples consists of fragments of some 12 exposed, and additional unprepared, abdominal ribs. The fragments are gently curved and slightly flattened hollow rods with oval cross-sections. The cross-sections measure between 5 and 10 mm by between 4 and 6 mm and show an outer layer of solid bone surrounding a central area of more cancellous bone. Nothing is currently known of the arrangement or extent of the gastralia.

OSTEODERMS

Osteoderms (= dermal armour/ossifications, scutes) are not generally thought to have been present in the earliest archosaurs, but are instead currently considered to be a synapomorphy of the more derived group *Euparkeria*+Proterochampsidae+crown-group archosaurs (e.g. Benton & Clark 1988; Sereno 1991). Three specimens of *Erythrosuchus africanus* suggest, however, that osteoderms have a wider distribution among archosaurs.

In his description of the holotype SAM–905, Broom (1906) briefly mentioned an element that he believed to be an unpitted dermal ossification (see also footnote in Charig & Reig 1970: 133). A re-examination of this material has unfortunately failed to identify which element Broom was referring to. Juul (1994: 6) reported the presence of rounded osteoderms in BPI 5207, but that ‘the arrangement of these is uncertain’. The presence of osteoderms in BPI 5207 was not noted during examination of that specimen in the course of this study. The third specimen is BMNH R3592, which includes two possible

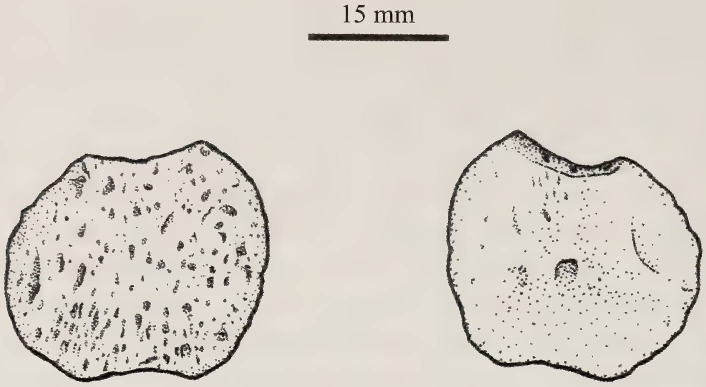

Figure 36

Erythrosuchus africanus, isolated osteoderm of BMNH R3592 in presumably outer and inner views.

osteoderms, neither of which was mentioned by Huene (1911). The first example, shown in Figure 36 and not closely associated with any other element, is undoubtedly an osteoderm. It is nearly circular and strongly flattened, with a pitted and well-ossified, presumably outer surface, and a less completely finished inner surface. A small transverse break reveals a cancellous interior with three internal canals extending parallel to the long axis of the element (presumably also the long axis in life position). The second BMNH R3592 example is closely associated with the caudal vertebrae (Fig. 27B). It is not resting above a neural spine, but is instead preserved attached to the left lateral surface of the sixteenth caudal vertebra. It is oval-shaped and has a strongly concave, presumably outer surface, and a less concave inner surface. This more poorly preserved example shows no indication of pitting on the outer surface, but it is also interpreted here as an osteoderm. There is no evidence of any non-*Erythrosuchus* archosaur material being collected with BMNH R3592.

Despite these possible examples of osteoderms, stronger evidence for their presence in *Erythrosuchus africanus* is clearly required. The two described examples were not found in life position nor do they exhibit a consistent morphology, not that one should necessarily be expected. Very few specimens of *E. africanus* preserving articulated postcranial material have been collected. The absence of intercentra (that were certainly present in life) in the more complete postcranial specimens suggests that the lack of osteoderms should not necessarily be taken as evidence of absence. An extensive set of osteoderms are preserved in close association with the recently discovered erythrosuchid skeleton (Pickford 1995) from the Omingonde Formation of Namibia (M. Kotzé, personal communication 1999).

IMPLICATIONS

SKELETAL RECONSTRUCTION

A diagrammatic reconstruction of the skeleton of *Erythrosuchus africanus* is presented in Figure 37. This is based largely on the specimens SAM–905, BPI 5207, and BMNH R3592. It represents the approximate proportions of the whole animal, and should not be taken as a statement on locomotion or gait in the absence of a detailed functional study. The skeletal reconstruction by Huene (1911) looks ungainly with an excessively large skull, but the proportions he presented are approximately correct according to this revision. Based on BMNH R3592, the estimated total body length is just over 4 metres. Some incomplete specimens suggest a maximum size greater than this. Preserved among the BMNH R3592 material is a fragment of a dorsal neural arch that measures 140 mm between the tips of the anterior and posterior zygapophyses, and with a neural spine some 85 mm long at its base—an estimated total body length of 4.75–5 m, based on extrapolation of proportions of the individual represented by the bulk of BMNH R3592.

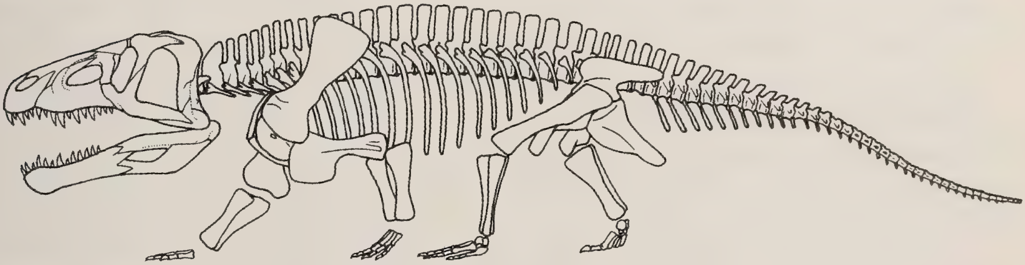

Figure 37

Erythrosuchus africanus, restoration of whole skeleton in left lateral view. Excepting the carpals, all unknown elements (several vertebrae, interclavicle, clavicles, and manual phalanges) have been completely restored. This figure is intended to show the relative proportions of a skeleton approximately the size of BMNH R3592 (total length 4 m+), and should not be taken as a statement on limb mechanics or gait.

CRANIAL AND MANDIBULAR KINESIS

Although some of the cranial (including the braincase—Gower 1997) and mandibular elements have features that suggest that they formed movable joints with other elements in life, the available evidence is interpreted as showing that the skull and mandible were not kinetic to any notable extent. For example, the dorsal surfaces of the laterosphenoids are rounded (Gower 1997) and these articulate with depressions on the ventral surface of the skull roof that are larger than the laterosphenoids, but these joints could not have been movable in the adult skull because the interdigitating frontal-parietal suture indicates that it was a stiff structure in this region, and the braincase is otherwise in close contact with the parietal. Similarly, the rounded head of the quadrate could not have rotated within the squamosal depression in which it lies because the squamosal-quadratojugal and quadratojugal-quadrate junctions seem to have been fairly firm. The premaxilla was not firmly sutured to any element, but movement of this element in isolation was probably limited, at most, to some sliding along the long axis of the premaxillary peg that articulates with the pit on the anterior margin of the maxilla. The mandibular symphysis was not an osteologically specialized region and some relative movement between the jaw rami may have been possible, but the interlocking of the three dentary posterior processes with the posterior elements of the mandible would have clearly limited movement from occurring within each individual ramus.

The presence of potentially movable articulations between elements in an essentially akinetic skull and mandible has also been noted in the rauisuchian *Batrachotomus kupferzellensis* (Gower, 1999). This pattern of joint may have been important in allowing minor, passive movement within the functioning adult skull (e.g. in transmitting forces encountered during feeding), may have been a remnant from a more kinetic juvenile skull, or is perhaps largely misleading in terms of movement in life.

TAXONOMY

Despite the relative wealth of erythrosuchid material that has been collected from the *Cynognathus* Assemblage Zone of South Africa, it has never been suggested that the material represents more than one species. This is in marked contrast to the South African proterosuchid archosaur material from the *Lystrosaurus* Assemblage Zone, which has been the subject of much taxonomic debate (see Charig & Reig 1970; Cruickshank 1972; Welman & Flemming 1993; Welman 1998). The difference probably lies in the fact that debates about the proterosuchid material has centred on a series of variably sized, essentially complete, and fully articulated skulls—only two of which are known for *Erythrosuchus*. The detailed re-examination of the South African erythrosuchid material that formed the basis of the redescription of *Erythrosuchus* presented here, has also allowed an assessment of the possibility that the material represents more than one species.

A number of small variations in morphology have already been noted in the above description. Some of these can probably be explained as ontogenetic or individual variation, such as the shape and relative size of the deltopectoral crest, the slenderness of the scapula, and the anterior projection of the dorsal iliac crest. The lower ratio between the height and length, and the more circular articular surfaces of the cervical centra in specimens (BPI 4680, SAM–3028) from individuals that are smaller than BMNH R3592 is another possible example of growth-related changes in morphology. Other, possibly non-growth related variations present more of a problem in that they are seen in incomplete specimens that preclude detailed comparisons. For example, slight differences exist among the skull roofs of BMNH R3592, BPI 5207, NM QS1473, and

GHG AK82–22 and among the maxillae of BMNH R3592, BPI 4680, 2529, 4540, and SAM–K1098, but two of the skull roofs and three of the maxillae represent all that is known of these particular specimens.

The main variations that can not be clearly correlated with growth are noted here: postfrontal excluded from orbit on ventral surface by frontal-postorbital contact (clearly seen in NM QS1473, but probably absent in BMNH R3592); depression on underside of skull roof surrounding dorsal orbit border (present in BMNH R3592; absent in NM QS1473); posteromedial edge of dorsal surface of postfrontals (angular in BMNH R3592 and BPI 5207; more curved in NM QS1473); dorsal frontal-parietal suture (straight in BPI 5207; curved in NM QS1473); shape of antorbital fenestra (generally oval, but possibly more circular in BPI 3893); maxillary projection notching the border of the antorbital fenestra (only seen in BMNH R3592 and possibly SAM–K1098); maxillary dorsomedial pit(s) (see description above); position of internal carotid foramina on basisphenoid (close to the midline in BMNH R3592; further apart in UMCZ T700—Gower 1997).

All of these differences are slight, and covariance can not yet be studied. I support Parrish (1992) in his recommendation that it is most prudent to currently retain all of this material in a single species. As more complete material is collected and prepared, allowing extensive comparisons between specimens, this may need to be revised. More specimens might eventually make a quantitative assessment of the material worthwhile. A future move to distinguish multiple species would probably present problems in that the holotype (SAM–905) of *Erythrosuchus africanus* consists of postcranial material only. Cranial remains are currently assigned to *E. africanus* on the basis of their similarity to specimens such as BMNH R3592 that consist of skull material plus postcranial remains that resemble those of SAM–905.

Tatarinov (1961) referred the Russian species *Vjushkovia triplicostata* and *Garjainia prima* to *Erythrosuchus*, an assignment rejected by some subsequent taxonomic assessments of early archosaurs (e.g. Charig & Reig 1970; Charig & Sues 1976; Sennikov 1995) and here. Another species of *Erythrosuchus* from Russia has since been described by Ochev (1980) as *E. magnus*. Sennikov (1995) subsequently transferred this species to the new genus *Uralosaurus*. The material consists of a pterygoid, an incomplete dentary, and a few isolated teeth and incomplete vertebrae (see Gower & Sennikov 2000). Ochev partly based his referral of this material to *Erythrosuchus* on similarities to the Russian *Vjushkovia triplicostata* and *Garjainia prima*—accepting Tatarinov's synonymy of these genera with the South African *Erythrosuchus* (rejected here). A re-examination of the material in question shows it to be similar to those elements of known erythrosuchids with some slight differences (e.g. more curved dentary with low tooth count). The vertebral centra are as tall or taller than they are long and clearly bevelled ventral edges, probably for articulation with intercentra, can be seen on at least the anterior cervical example. This material possibly represents an erythrosuchid distinct from those already known from Russia and South Africa, but it is very incomplete, poorly known, and the association of the separate specimens is uncertain.

Based on current knowledge of early archosaur osteology, there is no convincing intrinsic evidence for the presence of more than one species of *Erythrosuchus*. To date, specimens of *Erythrosuchus* have not been found outside South Africa. The discovery in Namibia of a partial skeleton with skull and mandible of a 'proterosuchian cf. *Erythrosuchus africanus*' (Pickford 1995: 60) represents the first possible exception to this. This is perhaps the most complete skeleton of an erythrosuchid yet collected, and it will probably prove to be very important whether or not it represents *E. africanus*. Study of this material is now underway (M. Kotzé and R. M. H. Smith, personal communication 1999).

PHYLOGENY

In recent times (at least since Charig & Reig 1970), *Erythrosuchus* has consistently been recognized as a member of the Erythrosuchidae—a clade including other Lower to Middle Triassic archosaur taxa such as *Shansisuchus* from China and *Garjainia prima* from Russia. Cladistic analyses have also reached a consensus that the Erythrosuchidae lie outside the archosaurian crown group (Gower & Wilkinson 1996; Bennett 1996), but there have been very few explicit phylogenetic considerations of the internal relationships among erythrosuchids. Parrish (1992) conducted the first study and hypothesized that, within the Erythrosuchidae, *Erythrosuchus* is more closely related than is *Garjainia prima* to a clade composed of *Shansisuchus+Vjushkovia* (*V. triplicostata+V. sinensis*). Gower & Sennikov (1996*b*, 1997) did not consider *V. sinensis* or *G. prima*, but they presented evidence supporting an alternative hypothesis in which *Shansisuchus* is more closely related to *E. africanus* than it is to *V. triplicostata*. Gower & Sennikov (2000) have since presented evidence that *V. triplicostata* should be considered a junior synonym of *G. prima*.

A major proportion of Gower & Sennikov's (1996*b*, 1997) phylogenetic data came from the braincase. This current study includes further support for the hypothesis that *Shansisuchus* and *Erythrosuchus africanus* share a more recent common anestor with each other than either taxon does with *Garjainia prima* (= *Vjushkovia triplicostata*). For example, the Chinese and South African taxa share a premaxillary 'peg' that articulates with a maxillary 'socket', a pleat/tuck on the posterior surface of the ventral process of the squamosal, a short and low retroarticular process, and a quadratojugal that is nearly excluded from the border of the lower temporal fenestra (Young 1964; Cheng 1980; personal observation)—derived features absent in *G. prima* (personal observation).

Understanding of erythrosuchid interrelationships remains at a preliminary stage, and several taxa have yet to be considered in explicit phylogenetic analyses: for example, *Guchengosuchus shiguaiensis* Peng, 1991 and *Chalishevia cothurnata* Ochev, 1980. The affinity of *Vjushkovia* (= *Youngosuchus* Sennikov *in* Kalandadze & Sennikov, 1985) *sinensis* is currently in doubt, and Sennikov (*in* Kalandadze & Sennikov 1985) has suggested that it is a rauisuchian rather than an erythrosuchid.

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ABBREVIATIONS

INSTITUTIONS

AMNH	American Museum of Natural History
BMNH	Natural History Museum, London
BPI	Bernard Price Institute for Palaeontological Research, Johannesburg
DMSW	D.M.S. Watson Collection
GHG	Geological Survey, Pretoria
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing
NM	Nasionale Museum, Bloemfontein
PIN	Palaeontological Institute, Moscow
RC	S.H. Rubidge Collection, Wellwood, Graaff Reinet
SAM	South African Museum, Cape Town
UMCZ	Cambridge University Museum of Zoology
VH	Vienna Hoffmuseum

MORPHOLOGY

a	angular
acc	accessory (3rd) rib head
acet	acetabulum
acr	acromion process
ad	adductor crest
af	adductor fossa
am	area of origin of *m. ambiens*
aofo	antorbital fossa
ap	anterior process of rib
ar	articular
atna	atlas neural arch
ax	axis vertebra
bo	basioccipital
bs	basisphenoid
c	coronoid
cap	capitulum
ch	choana
chty	chorda tympani branch of facial nerve, route of
cnc	cnemial crest
co	coracoid
cof	coracoid foramen
com	surface finished with compacta bone
cot	channel for olfactory tract
cu	cultriform process of parasphenoid
d	dentary
d.	dorsal part of ......
dc	central posterior process of dentary
dd	dorsal posterior process of dentary

dep	depression
di	(facet of) diapophysis
dpc	deltopectoral crest
dv	ventral posterior process of dentary
e	epipterygoid
ec	ectopterygoid
ectg	ectepicondylar groove
en	external naris
eo	exoccipital
eth	foramen for medial ethmoidal artery
f	frontal
fi	fibula
fm	foramen magnum
for	foramen/foramina
gl	glenoid fossa of shoulder girdle
gr	groove
ha	haemal arch
ic	intercentrum
icg	intercondylar groove
if	area of insertion of *m. iliofibularis*
ilf	area of insertion of *m. iliofemoralis*
imf	infra-Meckelian foramen
itf	intertrochanteric fossa
j	jugal
l	lacrimal
la	lamella
lf	lacrimal foramen
lmf	lateral mandibular fenestra
ls	laterosphenoid
m	maxilla
ma	muscle attachment scar
mas	ascending process of maxilla
mec	Meckelian canal
ml	thin lateral part of maxilla
mm	thick medial part of maxilla
mp	maxillary pit/neurovascular channel
mpit	maxillary pit for premaxillary peg
mpr	maxillary projection
n	nasal
nf	nutrient foramina
nfl	nasal anteroventral flange
no	notch
ob	obturator foramen
os	osteoderm
p	parietal
pal	palatal process
par	(facet of) parapophysis
pbp	parabasal process

pf	postfrontal
pi	pit for attachment of *m. puboischiotibialis*
pif	pineal fossa
pit	pit
pl	palatine
pm	premaxilla
pmp	premaxillary peg
po	postorbital
pop	popliteal space
popr	paroccipital process
pp	postparietal
pra	prearticular
prf	prefrontal
prfp	prefrontal pillar
pro	proatlas
prq	pterygoid ramus of quadrate
pt	pterygoid
ptub	parietal tubercle
pv	posteroventral process of parietal
q	quadrate
qh	quadrate head
qj	quadratojugal
qjc	quadrate posterodorsal concavity
qpt	quadrate ramus of the pterygoid
r.	right
rap	retroarticular process
ri	rib
s.	surface/area/groove for articulation with ......
sa	surangular
saf	surangular foramen
sc	scapula
so	supraoccipital
sp	splenial
sq	squamosal
stf	supratemporal fenestra
sup	supinator process
supr	supinator ridge
sym	area of mandibular symphysis
t	tibia
tc	tubercle
to	tooth
tr	transverse process
tro	trochanter
tu	‘tuck’ or ‘pleat’ in posterior margin of squamosal
tub	tuberculum
v.	ventral part of ......
?	tentative identification
I–IV	metacarpal number

APPENDIX I

Material of *Erythrosuchus africanus*

SAM–905	Incomplete postcranial skeleton (holotype).
SAM–912	Incomplete pelvic girdle.
SAM–978	Fragmentary skull material. A non-*Erythrosuchus* maxilla, probably not part of the original specimen (different matrix), was also stored under this number.
SAM–1315	Single cervical vertebra.
SAM–3028	Incomplete postcranial material.
SAM–3612	Incomplete braincase.
SAM–11330	Skull roof fragments.
SAM–K1098	Incomplete left maxilla.
SAM–K1118	Incomplete posterior of skull and epistropheus.
SAM–PK–K10025	Incomplete postcranial skeleton.
BPI 2094	Fragmentary left maxilla.
BPI 2096	Right pes, tarsus and distal crus.
BPI 2529/322	Left maxilla.
BPI 2734	Jaw fragments.
BPI 3893	Virtually complete, largely unprepared skull.
BPI 4526	Left premaxilla.
BPI 4539	Fragmentary left maxilla.
BPI 4540	Left maxilla.
BPI 4553	First and fifth left metatarsal.
BPI 4645	Posterior part of skull roof and incomplete braincase.
BPI 4649	Fourth right metatarsal.
BPI 4680	Extensive but incomplete skull, braincase, and postcranial material.
BPI 5207	Complete skull.
GHG 7433MI	Small partial skeleton, possibly a juvenile *Erythrosuchus*.
GHG AK82–22	Incomplete skull roof.
NM QS1473	Skull roof.
BMNH R533	Two articulated dorsal vertebrae.
BMNH R533a	Neural arch of dorsal vertebra.
BMNH R533b	Incomplete dorsal vertebra.
BMNH R533c	Vertebral fragment.
BMNH R533d	Incomplete cervical vertebra.
BMNH R533e	Vertebral fragment.
BMNH R533f	Three consecutive caudal vertebrae.
BMNH R533g	Distal fragment of scapula.
BMNH R533i	Fragments of scapula and distal left femur.
BMNH R533x	Fragments of lower jaw and ilium.
BMNH R533?	Distal fragment of ulna.
BMNH R2790	Incomplete left mandible.

BMNH R2791	Single cervical vertebra.
BMNH R2792	Condylar fragment of left quadrate.
BMNH R2793	Vertebral fragments.
BMNH R2794	Dorsal part of quadrate and postcranial fragments.
BMNH R2795	Incomplete parietal posteroventral process and postcranial fragments.
BMNH R2809	Cast of left femur and tibia. Originals reportedly in Albany Museum, Grahamstown, South Africa.
BMNH R3592	Incomplete, but extensive skull, mandible, and postcranial material of single individual with at least some metacarpals from second, smaller individual.
BMNH R3592a	Left distal crus, tarsus, and metatarsus (formerly DMSW R525).
BMNH R3755	Vertebral fragments.
BMNH R3759	Incomplete postcranial material, mostly vertebral but also proximal end of eft femur.
BMNH R3762	Good but incomplete postcranial material. The specimen includes a distal fragment of a humerus and a vertebra (with notochordal centrum) which are not referable to *Erythrosuchus*.
BMNH R3763	Good right scapula and further fragmentary postcranial material.
BMNH R3764	Left pubis.
BMNH R3776	Neural arch fragments.
BMNH R7888	Two incomplete dorsal vertebrae.

Several specimens in the BMNH collection are unnumbered.

(i) Proximal fragment of left tibia, currently together with BMNH R2790, but not mentioned by Seeley (1894).
(ii) A cervical and sacral vertebra and a sacral rib.
(iii) Anterior fragment of iliac crest.
(iv) Complete right ilium.

BMNH R8667	Mid-dorsal vertebrae (formerly part of BMNH R3592)

UMCZ T666	Right ischium, formerly DMSW R389.
UMCZ T675	Single sacral rib, formerly DMSW R460.
UMCZ T678	Two anterior caudal vertebrae, formerly DMSW R488.
UMCZ T682	Isolated articular, formerly DMSW R520.
UMCZ T700	Crushed and poorly preserved braincase, formerly DMSW R417.

AMNH 5594	Incomplete skull roof.
AMNH 5595	Humeral fragments.
AMNH 5596	Scapula and coracoid.
AMNH 5597	Incomplete humerus and tibia.

None of these AMNH specimens were examined for this study.

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UPPER CRETACEOUS (TURONIAN–CONIACIAN) AMMONITES FROM SÃO NICOLAU, ANGOLA

by

MICHAEL ROBERT COOPER

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UPPER CRETACEOUS (TURONIAN–CONIACIAN) AMMONITES FROM SÃO NICOLAU, ANGOLA

by
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(With 28 figures)

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ABSTRACT

The ammonite fauna from a condensed Turonian–Lower Coniacian succession is described from São Nicolau in the southern part of the Moçamêdes Desert. Genera represented include *Hypophylloceras*, *Tetragonites*, *Gaudryceras*, *Anagaudryceras*, *Puebloites*, *Baculites*, *Damesites*, *Mesopuzosia*, *Mossamedites*, *Kossmaticeras*, *Tongoboryceras*?, *Placenticeras*, *Vascoceras*, *Morrowites*, *Forresteria*, *Prionocyclus*, and *Prionocycloceras*. The species *Baculites klingeri* is new.

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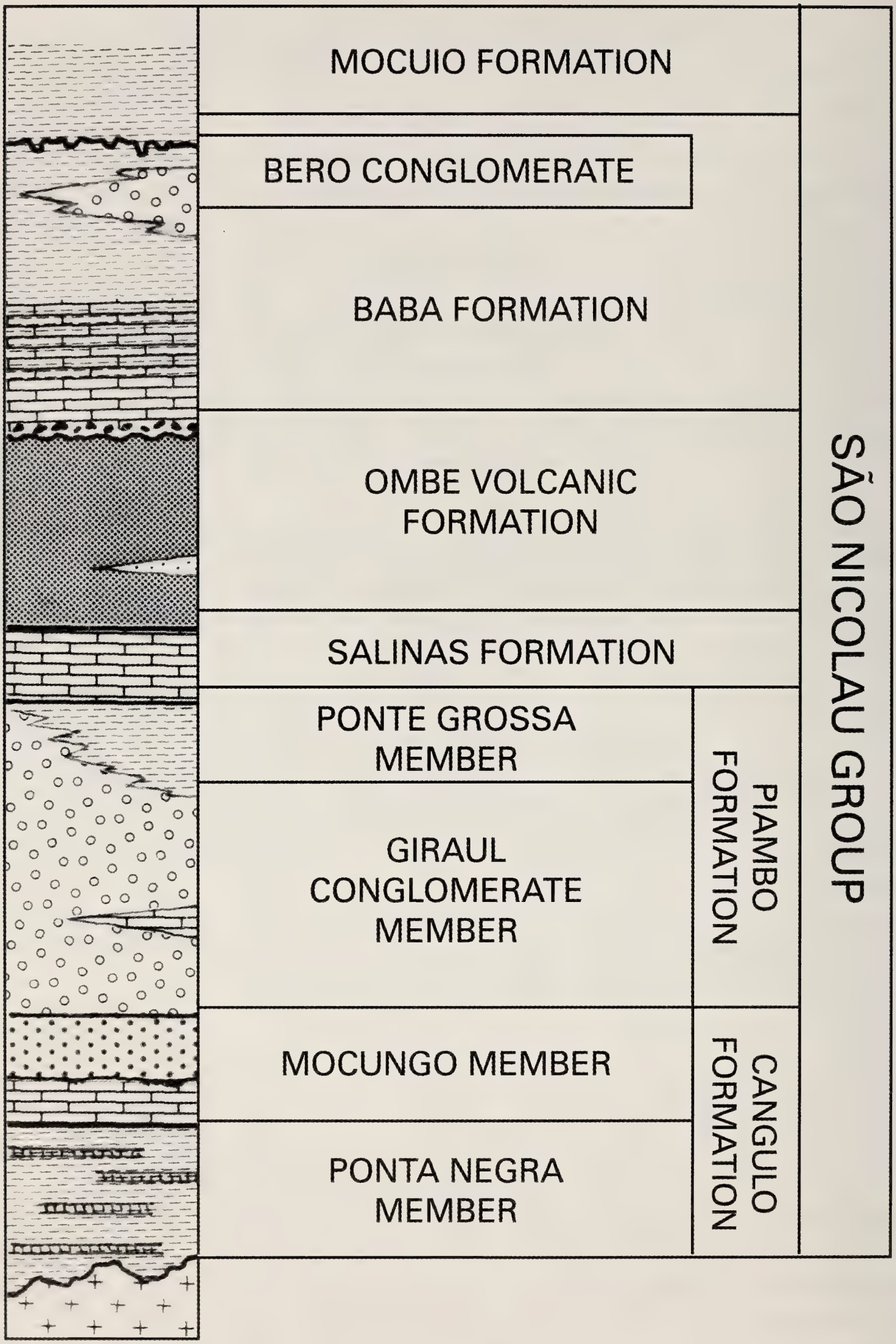

Figure 1

The Cretaceous lithostratigraphy of the Moçamêdes basin.

INTRODUCTION

Although diversified Albian and Maastrichtian ammonite assemblages have long been known from Angola, the mid-Cretaceous faunas are less well understood. Haughton (1925: 264) reported 'doubtfully Turonian' ammonites from the Cuanza basin; these are in the South African Museum and form part of the same Upper Turonian fauna recorded subsequently by Basse (1963). Thiele (1933) identified Lower Turonian *Mammites conciliatus* (Stoliczka) in faunas from Novo Redondo, but this is a misidentification of the outer horned whorls of Middle Cenomanian *Cunningtoniceras*. Haas (1942) figured a poorly preserved *Romaniceras* from north of Cabiri in the Cuanza basin, and Hoppener (1958: 80) recorded *Coilopoceras cacobaensis* (a *nomen nudum*) from Tuenza in the Cuanza basin. Basse (1963) described a badly crushed Late Turonian fauna from Cabo Ledo, including *Subprionocyclus* and *Puebloites*, and Howarth (1968) documented a mid-Turonian ammonite fauna from Ponta Grossa, just north of the present locality; the latter fauna includes several of the species recorded here.

Cooper (1973) reported on Middle Cenomanian ammonites from Novo Redondo and, subsequently, described uppermost Cenomanian–basal Turonian faunas from Salinas (Cooper 1978*a*); he also summarized the mid-Cretaceous (Albian–Coniacian) stratigraphy of Angola, figuring some of the mid-Cretaceous faunas (Cooper 1978*b*). Collignon (1977) described *Kamerunoceras almeidai* Collignon, *Collignoniceras reali* Collignon, *Pseudaspidoceras armatum* Pervinquière, *Mammites nodosoides* (von Schlotheim) and *Hoplitoides* aff. *ingens* Von Koenen, but without providing stratigraphic or locality data.

The most recent work, by Howarth (1985), documents a Cenomanian–Lower Turonian fauna from the environs of Novo Redondo.

STRATIGRAPHY

The Cretaceous succession of the Moçamêdes basin is well known following the studies of Carvalho (1958, 1960, 1961). Cooper (1976, 1978*b*) applied formal lithostratigraphical nomenclature and assigned the succession to the São Nicolau Group (Fig. 1). The present collections come from the upper part of the Salinas Formation (Fig. 2), a marine succession of uppermost Cenomanian to early Coniacian age that, in general, follows conformably on underlying strata. It is overlain, perhaps disconformably (Cooper 1972), by basalts, analcime basanites and andesites (Andrade 1957) of the Ombe Formation, a Middle Coniacian to Lower Santonian volcanic suite.

The collections which form the basis of this paper were made in the spring of 1972, from erosion gullies incising the sea cliffs east of the army post at São Nicolau. The stratigraphy at this locality (Fig. 2) shows several features common to condensed sequences, including negligible thickness, faunal enrichment and associated stromatolites (Cooper 1972). The Lower Turonian to Lower Coniacian succession at this locality is condensed into only 6 m.

Associated with the ammonites are diverse bivalves and gastropods, including *Acanthotrigonia shepstonei* (Griesbach), *Veniella forbesiana* (Stoliczka), *Pseudocucullaea*

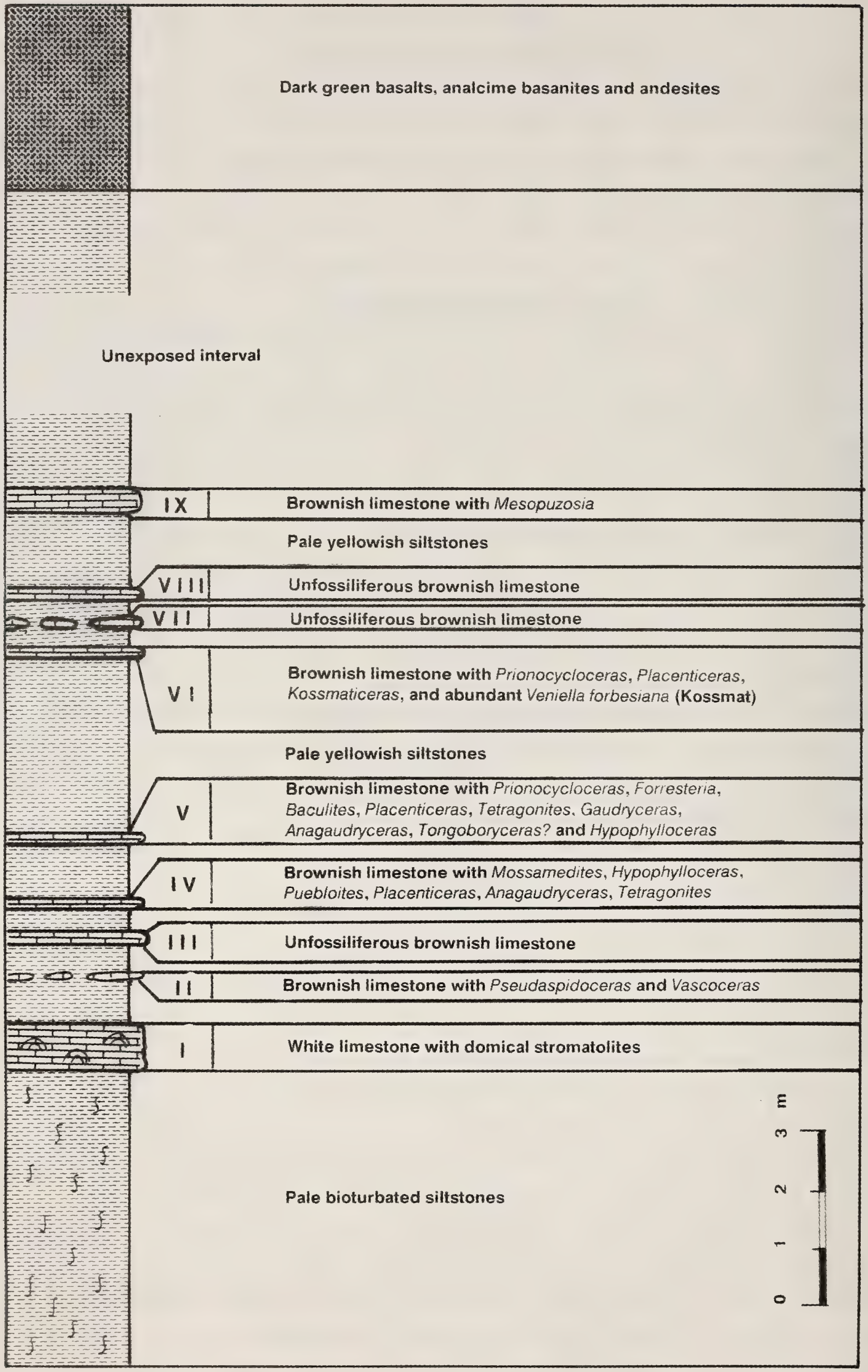
Dark green basalts, analcime basanites and andesites
Unexposed interval
IX
Brownish limestone with *Mesopuzosia*
Pale yellowish siltstones
VIII
Unfossiliferous brownish limestone
VII
Unfossiliferous brownish limestone
VI
Brownish limestone with *Prionocycloceras*, *Placenticeras*, *Kossmaticeras*, and abundant *Veniella forbesiana* (Kossmat)
Pale yellowish siltstones
V
Brownish limestone with *Prionocycloceras*, *Forresteria*, *Baculites*, *Placenticeras*, *Tetragonites*, *Gaudryceras*, *Anagaudryceras*, *Tongoboryceras?* and *Hypophylloceras*
IV
Brownish limestone with *Mossamedites*, *Hypophylloceras*, *Puebloites*, *Placenticeras*, *Anagaudryceras*, *Tetragonites*
III
Unfossiliferous brownish limestone
II
Brownish limestone with *Pseudaspidoceras* and *Vascoceras*
I
White limestone with domical stromatolites
Pale bioturbated siltstones
0 1 2 3 m

Figure 2

Measured section through the upper part of the Salinas Formation, west of São Nicolau.

lens Solger, *Trigonarca capensis* (Griesbach), *Protocardia umkwelanensis* (Etheridge), *Rastellum (Arctostrea)* sp., *Meretrix umzambiensis* Rennie, *Zaria bonei* (Baily), *Arrhoges* aff. *bailyi* (Etheridge), *Pseudomelania*? sp., *Semifusus* sp., and *Cryptorhytis* sp.

All the material referred to here is housed in the palaeontological collections of the South African Museum, Iziko Museums of Cape Town (SAM).

DIMENSIONS

Dimensions of specimens are given in millimetres, where D = shell diameter, W = whorl width, H = whorl height, and U = umbilical width. The abbreviation c. (= *circa*) is used where, due to damage to the shell, dimensions have been estimated. Figures in parentheses refer to dimensions as a percentage of the shell diameter.

SYSTEMATIC PALAEONTOLOGY

Class CEPHALOPODA Cuvier, 1797
Subclass AMMONOIDEA Zittel, 1884
Order PHYLLOCERATIDA Arkell, 1950
Suborder PHYLLOCERATINA Arkell, 1950
Superfamily PHYLLOCERATACEAE Zittel, 1884
Family **Phylloceratidae** Zittel, 1884
Subfamily Phylloceratinae Zittel, 1884
Genus *Hypophylloceras* Salfeld, 1924
Subgenus *Hypophylloceras* Salfeld, 1924

Type species

Phylloceras onoense Stanton, 1894; by original designation (Salfeld, 1924: 60).

Discussion

The writer follows a number of earlier workers (Birkelund 1965; Matsumoto & Morozumi 1980; Matsumoto 1984; Henderson & McNamara 1985; Cooper 1989) in according *Hypophylloceras* generic status.

Hypophylloceras (Hypophylloceras) sp. nov.?
Fig. 3A–B

Compare

Phylloceras cf. *ellipticum* Collignon (*non* Kossmat), 1956: 14, pl. 1 (fig. 1).

Material

With certainty only SAM–PCA1872, from Bed IV, although a crushed and poorly preserved specimen, SAM–PCA1772 from Bed V, may belong here also.

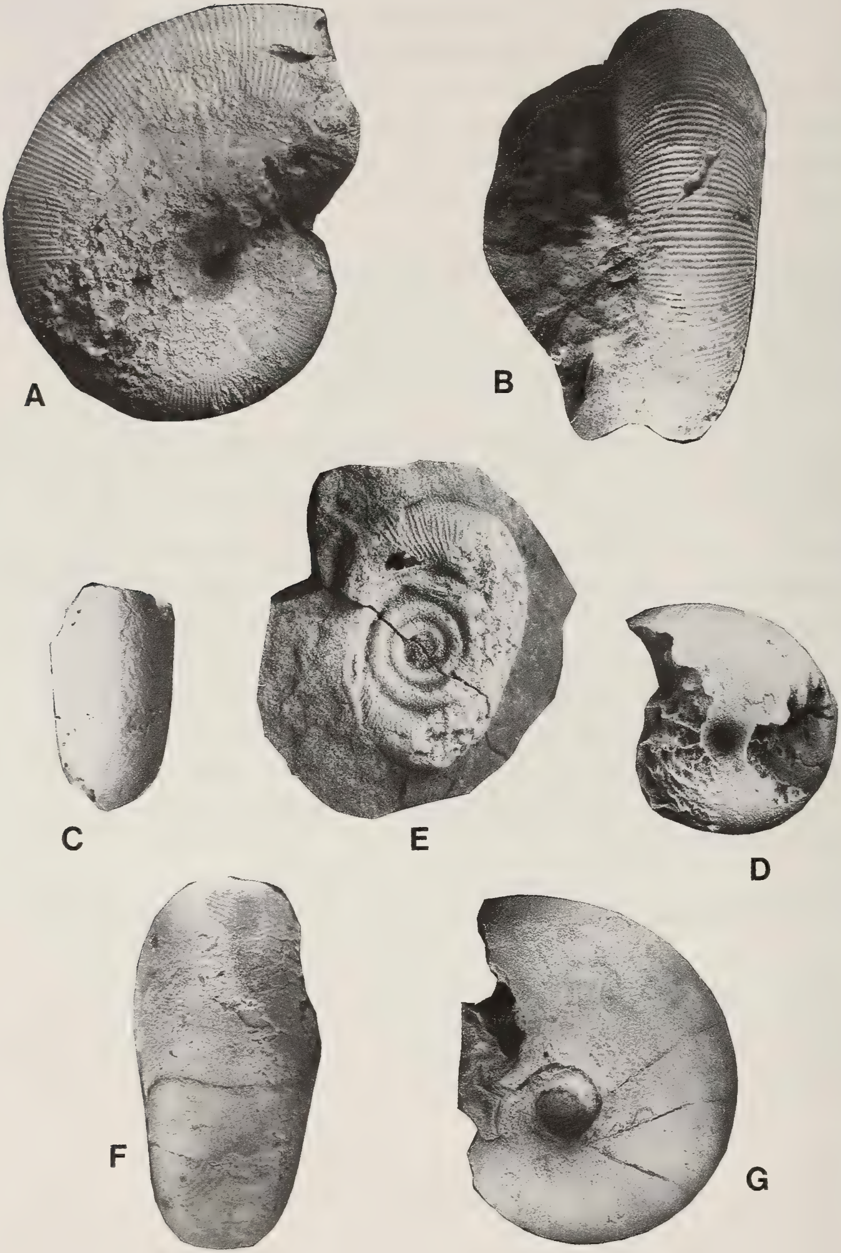

Figure 3

A–B. *Hypophylloceras (Hypophylloceras)* sp. nov.? × 1.5. Ventral and lateral views of SAM–PCA1872. C–D. *Damesites ainuanus* Matsumoto. × 1.5. Ventral and lateral views of SAM–PCA1756. E. *Gaudryceras mite* (von Hauer). × 1.5. Lateral view of SAM–PCA1750. F–G. *Tetragonites glabrus* (Jimbo). × 1.5. Ventral and lateral views of SAM–PCA1870.

Description

The shell is compressed, with virtually the entire preceding whorl covered. The umbilicus is very involute (5 per cent of the shell diameter), pit-like, with a sloping umbilical wall and subrounded shoulder. The whorl section is subovate, compressed (H/W = 1.36), with a narrow evenly arched venter and weakly convex flanks which converge slightly towards the venter. Maximum width is one-third of the way up the flank.

Ornament is lacking on the inner flanks but this is due, at least partly, to corrosion. On the outer flank there are 23 fine, weakly prorsiradiate to almost rectiradiate lirae in a distance equal to the whorl height, with at least 100 per half whorl. The lirae are as wide as the interspaces, faintly convex adorally, and cross the venter transversely. The suture is not displayed.

Measurements

Specimen	D	H	W	H/W	U
SAM–PCA1872	36.5	22.5 (61,6)	*c.* 16.5 (*c.* 45.2)	1.36	2.0 (5.4)

Discussion

The Angolan specimen most closely approaches the *Phylloceras* cf. *ellipticum* Kossmat figured by Collignon (1956: 14, pl. 1 (fig. 1)) from the Turonian of Madagascar, but is less inflated (the Madagascan specimen has a H/W ratio of 1.21). According to Kennedy & Klinger (1977*a*), the Malgash specimen is probably *Hypophylloceras improvisum* (Stoliczka) (1865: 113, pl. 58 (fig. 4)); the latter Cenomanian species, however, differs from the Angolan example in having flattened flanks. True *Hypophylloceras ellipticum* (Kossmat) (1895: 11, pl. 1 (fig. 2), pl. 6 (fig. 1)) is an Albian to Cenomanian species with elliptical whorl section, weak fold-like ribs and faint constrictions.

Turonian *Hypophylloceras bizonatus* (Fritsch) (*in* Fritsch & Schlönbach 1872: 40, pl. 14 (fig. 7)) and *H. masiaposense* (Collignon) (1956: 18, pl. 1 (fig. 7)) differ from the Angolan specimen in having flat subparallel flanks, a narrowly arched venter, and lirae which are straight or weakly concave adorally. Essentially, these are the characters that serve also to distinguish *H. woodsi* (van Hoepen) (Kennedy & Klinger, 1977*a*: 366, pl. 13 (figs 3–5), text–figs 4–5) and *H. compressum* (Matsumoto) (1942*b*: 675, figs a2, b2). Although Kennedy & Klinger (1977*a*) included *H. hoepeni* (Collignon) (1956) (Fig. 4E–F) in the synonymy of *H. woodsi*, the Malgash species differs in having more convex flanks and slightly rursiradiate (not prorsiradiate) lirae on the outer flank.

Campanian *Hypophylloceras lambertense* (Usher) (1952: 50, pl. 1 (figs 1–3)) is more compressed than the Angolan specimen, with lirae that commence at a lower level on the flanks, and Aptian *H. wiedmanni* Etayo-Serna (1979: 18, pl. 10 (fig. 3), text-fig. 3E) has flatter flanks, irregularly distributed umbilical pleats, and maximum width at the umbilical shoulder. Crushed *H. rousseli* (de Grossouvre) (Fig. 4A–B), from the Santonian of Sougraignes, France, differs from the present example in having steeper umbilical walls.

Stratigraphical occurrence

Hypophylloceras (Hypophylloceras) sp. nov.? is known with certainty only from the upper Middle Turonian of Angola although, possibly, it could range into the Coniacian.

Order LYTOCERATIDA Hyatt, 1889
Suborder LYTOCERATINA Hyatt, 1889
Superfamily TETRAGONITACEAE Hyatt, 1900
Family **Tetragonitidae** Hyatt, 1900
Genus *Tetragonites* Kossmat, 1895

Type species

Ammonites timotheanus Pictet, 1848; by original designation (Kossmat, 1895: 131).

Tetragonites glabrus (Jimbo, 1894)

Figs 3F–G, 5E–F

1894	*Lytoceras glabrum* Jimbo, p. 34, pl. 6 (fig. 2).
1895	*Lytoceras (Tetragonites) glabrum* Jimbo; Kossmat, p. 133.
1903	*Tetragonites glabrus* (Jimbo); Yabe, p. 43, pl. 7 (figs 2, 5).
1903	*Tetragonites sphaeronotus* (Jimbo); Yabe, p. 45, pl. 7 (fig. 1).
1942*a*	*Epigoniceras glabrum* (Jimbo); Matsumoto, p. 672.
1958	*Lytoceras (Tetragonites) jacksonense* Anderson, p. 186, pl. 10 (fig. 2).
1959	*Tetragonites glabrus* (Jimbo); Matsumoto, p. 149, pl. 39 (figs 72–73).
1967	*Tetragonites glabrus* (Jimbo); Jones, p. 25, pl. 2 (figs 1–12, 23–26).
1977*b*	*Tetragonites glabrus* (Jimbo); Kennedy & Klinger, p. 164.

Material

Six specimens; SAM–PCA1752 from Bed V, and SAM–PCA1857, 1870, 1873, 1882 and 1902 from Bed IV. None are complete but, where uneroded, they preserve recrystallized test.

Description

In SAM–PCA1870, the best-preserved individual (Fig. 3F–G), the shell is somewhat inflated and involute, with about 60 per cent of the preceding whorl covered. The umbilicus is narrow (21–26 per cent of the diameter), deep, with a vertical umbilical wall and evenly rounded umbilical shoulder. The flanks are slightly convex and converge to the broad, evenly rounded venter. The whorl section is semicircular, varying from somewhat depressed to as wide as high (H/W = 0.92–1.00).

Ornament is lacking save for growth striae and 5–6 constrictions per whorl, each backed by a low collar. The constrictions are strongly prorsiradiate, almost straight across the flanks, and reflex at the ventrolateral shoulders to cross the venter transversely, with a shallow adorally-concave sinus.

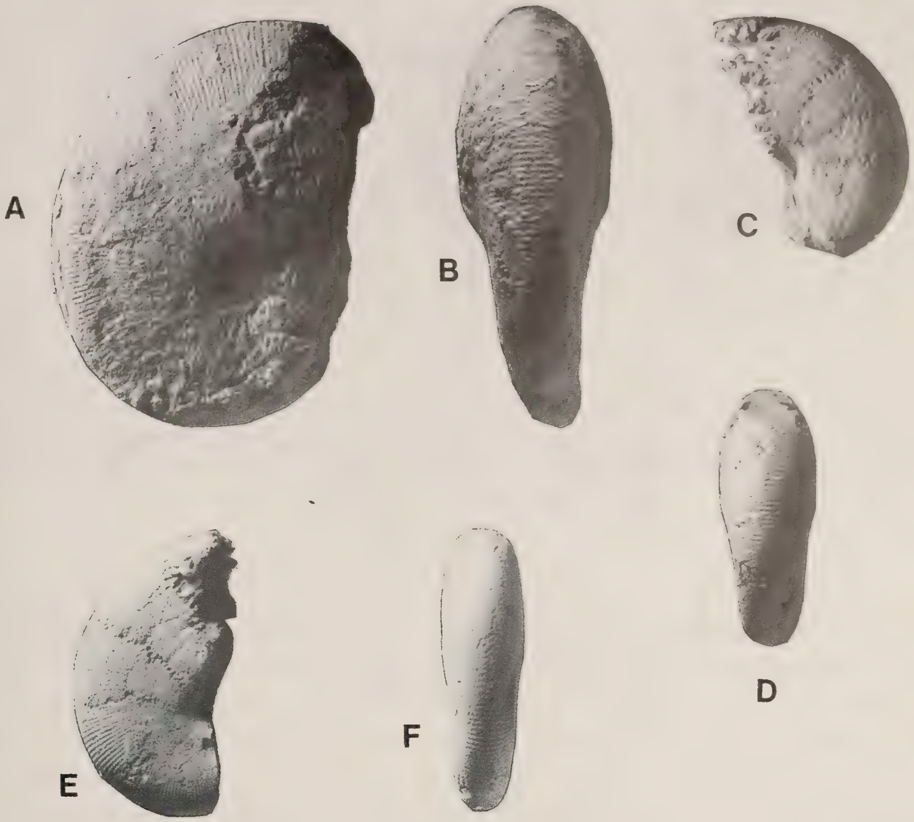

Figure 4

A–B. *Hypophylloceras (Hypophylloceras) rousseli* (de Grossouvre). The holotype, MHNP–R405, from the Santonian of Sougraignes (Aube). Figured by de Grossouvre (1894, pl. 24 (fig. 2)). C–D. *Hypophylloceras hoepeni infundibuliforme* (Collignon). The holotype, MHNP–R475, from the Lower Santonian of Tsianaloky, Madagascar. Figured by Collignon (1956, pl. 4 (figs 2–4)). E–F. *Hypophylloceras hoepeni hoepeni* (Collignon). The holotype, MHNP–R414, from the same locality as above. Figured by Collignon (1956, pl. 1 (figs 4–6)). All × 1.

Measurements

Specimen	D	H	W	H/W	U
SAM–PCA1870	33	16 (48)	*c.*16 (48)	1.00	7 (21)
"	22	12 (55)	*c.*12 (55)	1.00	5.5 (25)
SAM–PCA1875	32	16 (50)	?	?	7 (22)
"	23	11 (48)	12 (52)	0.92	6 (26)
SAM–PCA1752	35	18 (51)	19 (54)	0.94	7.5 (21)

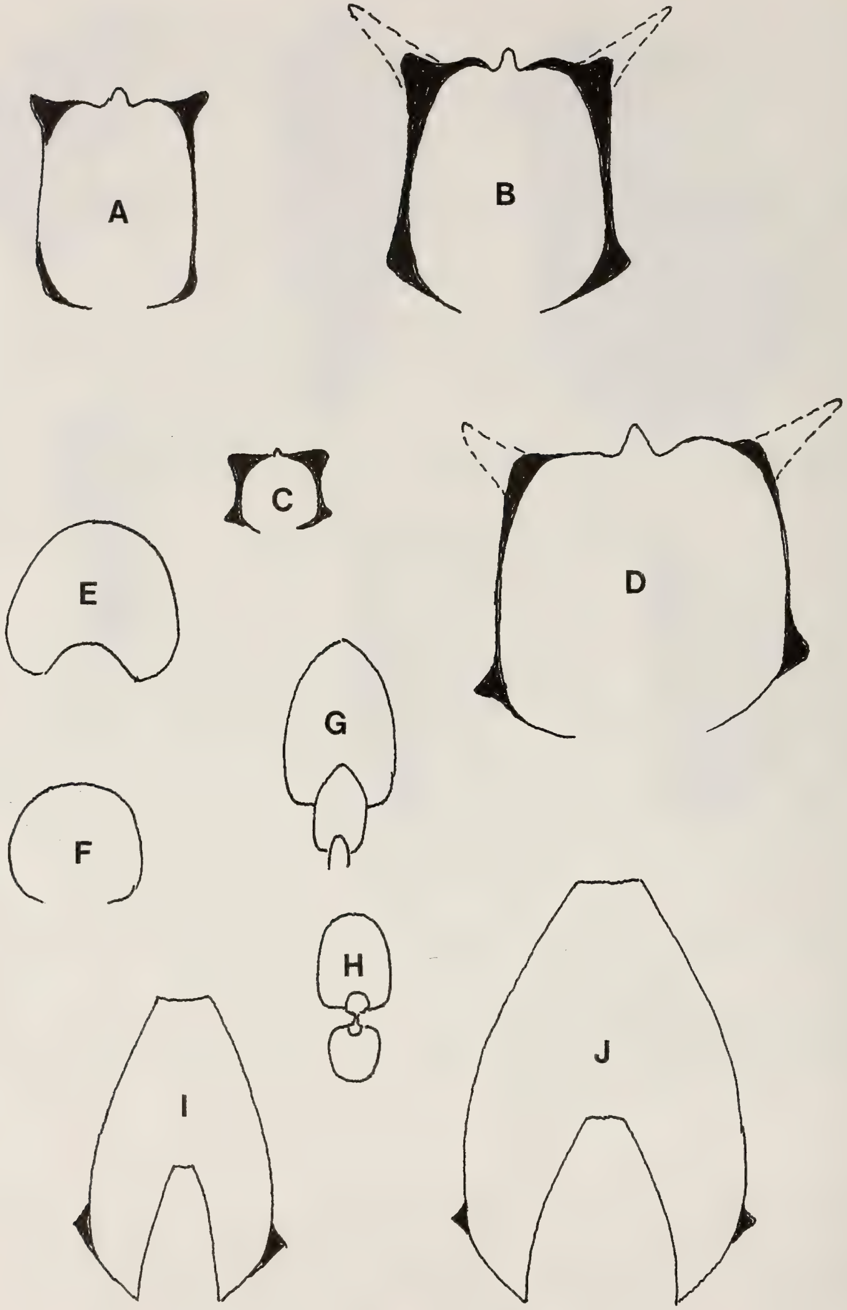

Figure 5

Whorl sections. A–D. *Prionocycloceras carvalhoi* (Howarth). A. SAM–PCA1754. B. SAM–PCA1944. C. SAM–PCA1942. D. SAM–PCA1758. E–F. *Tetragonites glabrus* (Jimbo). E. SAM–PCA1902. F. SAM–PCA1870. G. *Mossamedites serratocarinatus* (Kennedy & Cobban), SAM–PCA1862. H. *Damesites ainuanus* Matsumoto, SAM–PCA1750. I–J. *Placenticeras kaffrarium* Etheridge. I. SAM–PCA1952; J. SAM–PCA1869. All × 1.

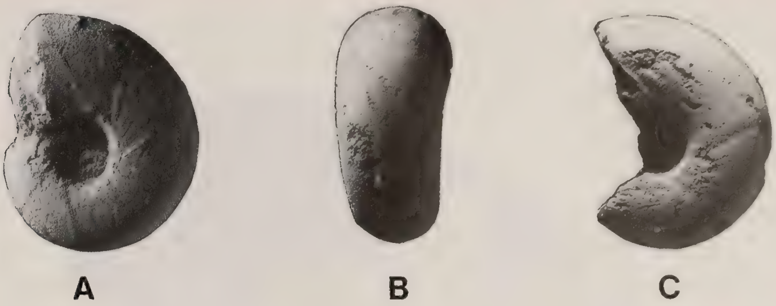

Figure 6

A. *Tetragonites beantalyensis* Collignon. The holotype, NHMP–R708, from the Coniacian of Beantaly, Madagascar. Figured by Collignon (1956, pl.10 (figs 1–2)). B–C. *Tetragonites mitraikyensis* (Collignon). The holotype, NHMP–R706, from the Upper Santonian of Mitraiky, Madagascar. Figured by Collignon (1956, pl. 11 (fig. 2)). All × 1.

Discussion

The characters of this species have been covered by Matsumoto (1959) and Jones (1967). At a comparable diameter, Madagascan *T. beantalyensis* Collignon (1956: 83, pl. 10 (fig. 1)) (fig. 6A) has a flatter venter than the Angolan material; it is said to be connected to contemporaneous *T. embergeri* Collignon (1956: 84, pl. 10 (figs 2–3)) by intermediates.

Tetragonites superstes van Hoepen (Kennedy & Klinger, 1977*b*: 162, figs 7–8, 12A–C) differs from the Angolan material in being more inflated, with only four faint constrictions at comparable diameter. Santonian *Tetragonites mitraikyensis* (Collignon) (1956: 86, pl. 11 (fig. 2)) is more involute, with a cylindrical outline in ventral view (fig. 6B–C).

Stratigraphical occurrence

Tetragonites glabrus (Jimbo) is a long-ranging species recorded from the Turonian–Lower Campanian interval (Matsumoto 1959) of Japan, California, Angola and Alaska.

Family **Gaudryceratidae** Spath, 1927

Genus *Gaudryceras* de Grossouvre, 1894

Type species

Ammonites mitis von Hauer (1866); by the subsequent designation of Boule *et al.* (1906: 11).

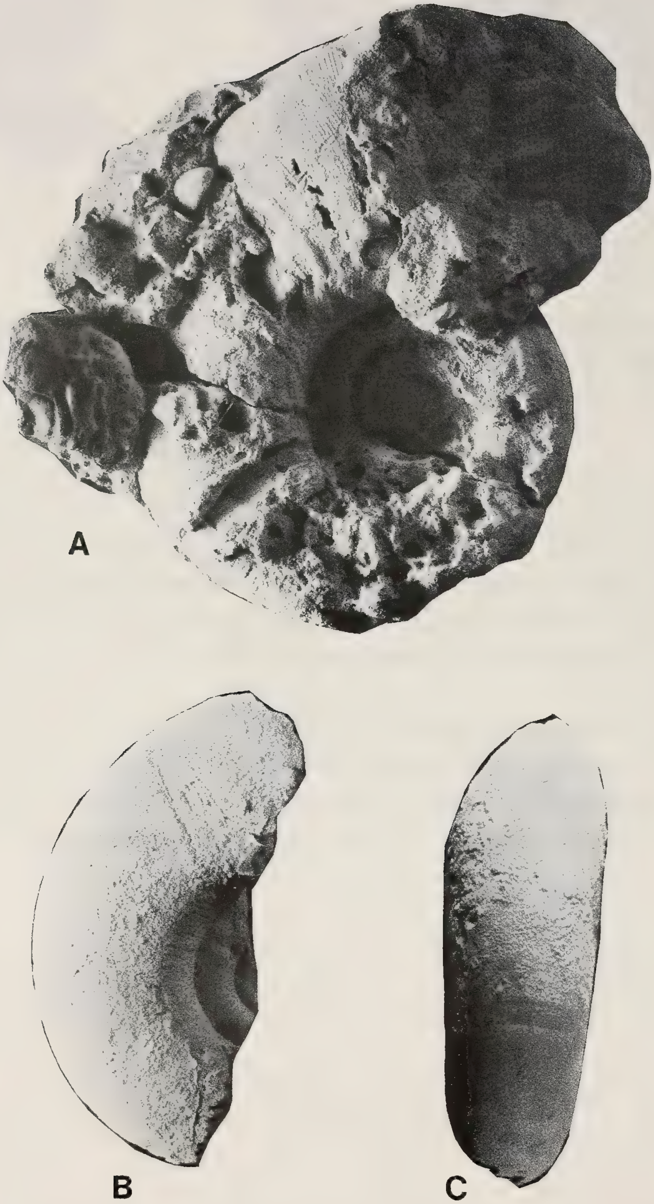

Figure 7

Anagaudryceras involvulum (Stoliczka). × 1. A. Lateral view of SAM–PCA1871. B–C. Lateral and ventral views of SAM–PCA1753.

Gaudryceras mite (von Hauer, 1866)
Fig. 3E

1866 *Ammonites mitis* von Hauer, p. 305, pl. 2 (figs 2–3).
1952 *Puzosia lytoceratoides* Haas, p. 8, figs 14–17.
1965 *Gaudryceras varagurense* Kossmat; Howarth, p. 361, pl. 4 (fig. 5), pl. 5 (figs 1–2).
1968 *Gaudryceras varagurense* Kossmat; Howarth, p. 4, pl. 1 (figs 6–7).
1979 *Gaudryceras mite* (von Hauer); Kennedy & Summesberger, p. 74, pl. 1 (fig. 1), pl. 2 (figs 1–2), text–fig. 1 (*cum synon.*).

Material

A single somewhat eroded specimen, SAM–PCA1750, with recrystallized test preserved, from Bed V.

Discussion

The extensive synonymy of this well-known species has been listed by Kennedy & Summesberger (1979). These workers, together with Haas (1952) and Howarth (1965, 1968), have all figured well-preserved examples of this species from Angola. The present specimen has little to add, save to extend the stratigraphic range of this species downward in Angola.

Stratigraphical occurrence

Gaudryceras mite (von Hauer) ranges from Turonian to Maastrichtian (Kennedy & Summesberger 1979), the present record being Lower Coniacian. It is known from Austria, the south of France, the Carpathians, northern Spain, Angola, Zululand, Madagascar, India and Antarctica.

Genus *Anagaudryceras* Shimizu, 1934

Type species

Ammonites sacya Forbes, 1846; by original designation.

Anagaudryceras involvulum (Stoliczka, 1865)
Fig. 7A–C

1865 *Ammonites involvulum* Stoliczka, p. 150, pl. 75 (fig. 1).
1865 *Ammonites sacya* (Forbes) Stoliczka, p. 154, pl. 76 (fig. 3 only).
1895 *Lytoceras (Gaudryceras) involvulum* (Stoliczka); Kossmat, p. 128.
1935 *Gaudryceras (Anagaudryceras) utaturense* Shimizu, p. 176.
1956 *Anagaudryceras involvulum* (Stoliczka); Collignon, p. 68.
1968 *Anagaudryceras involvulum* (Stoliczka); Howarth, p. 219, pl. 1 (figs 1–2).
1975 *Anagaudryceras involvulum* (Stoliczka); Kennedy & Juignet, p. 77, fig. 1.
1976 *Anagaudryceras involvulum* (Stoliczka); Juignet & Kennedy, p. 49, pl. 1 (figs 1–2).

1979 *Anagaudryceras involvulum* (Stoliczka); Kennedy & Klinger, p. 146.
1984 *Anagaudryceras involvulum* (Stoliczka); Wright & Kennedy, p. 50, pl. 2 (fig. 2), text-fig. 1C, F.
1985 *Anagaudryceras involvulum* (Stoliczka) Zaborski, p. 7, figs 3–4.

Material

Three specimens preserving recrystallized test, SAM–PCA1753 from Bed V, and SAM–PCA1867 and 1871 from Bed IV.

Description

The shell is evolute, compressed, with a wide shallow umbilicus (about 29 per cent of the shell diameter), inclined umbilical walls and gently rounded umbilical shoulders. The flanks are weakly convex, with maximum width just below midflank, and converge to the narrowly rounded venter. The whorl section is compressed oval (H/W = 1.21). Ornament comprises very fine dense lirae that, up to 70 mm diameter, are visible only with the aid of a hand lens. There are 3 weakly prorsiradiate, straight constrictions per half whorl.

Measurements

Specimen	D	H	W	H/W	U
SAM–PCA1753	*c.* 62	25.5 (*c.* 41)	21 (*c.* 34)	1.21	*c.* 18 (*c.* 29)

Discussion

This widespread species was recorded from the Ponta Grossa locality by Howarth (1968); he covered the essential differences with other species, as did Wright & Kennedy (1984) and Zaborski (1985).

Stratigraphical occurrence

Anagaudryceras involvulum (Stoliczka) ranges from Lower Cenomanian to Lower Coniacian (Wright & Kennedy 1984); the present material occurs both in the upper Middle Turonian and Lower Coniacian. It is reported from Japan, Nigeria, Angola, southern India, France and England.

Suborder TURRILITINA Besnosov & Mikhailova, 1983

Superfamily TURRILITACEAE Gill, 1871

Family **Hamitidae** Gill, 1871

Genus *Puebloites* Cobban & Scott, 1973

Type species

Helicoceras? *corrugatum* Stanton, 1894; by original designation (Cobban & Scott, 1973: 45).

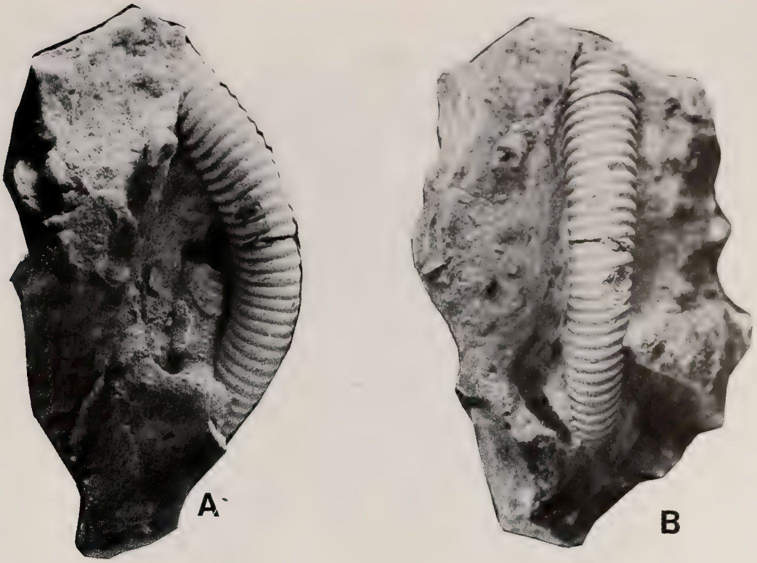

Figure 8

Puebloites greenhornensis Cobban & Scott. × 1.5. (A) Lateral and (B) ventral views of SAM–PCA1880.

Puebloites greenhornensis Cobban & Scott, 1973
Fig. 8A–B

?1967	*Scalarites* sp. indet.; Collignon, p. 32, pl. 18 (fig. 2).
1972	*Scalarites* sp.; Cooper, p. 248.
1973	*Puebloites greenhornensis* Cobban & Scott, p. 46, pl. 19 (figs 7–28).
?1982	*Glyptoxoceras* cf. *indicum* (Forbes); Renz, p. 73, pl. 22 (figs 7–8).

Material

A single specimen, SAM–PCA1880, preserving recrystallized test, from Bed IV.

Description

The specimen is a loose gently arched fragment with subelliptical whorl section (H/W = 1.05). Ornament comprises 5 strong annular ribs in a distance equal to the major diameter. These cross the dorsum and venter obliquely, becoming crowded on the dorsum. There are no flared ribs or constrictions, and the suture is not displayed.

Discussion

Although the general impression of *Puebloites greenhornensis* Cobban & Scott is of a more-densely ribbed form, the Angolan example falls within the range of variation displayed by the Colorado species. Early Turonian *P. spiralis* Cobban & Scott (1973: 46, pl. 18 (figs 1–5), pl. 19 (figs 1–6)) is more densely ribbed, with narrower sharper ribs, as is

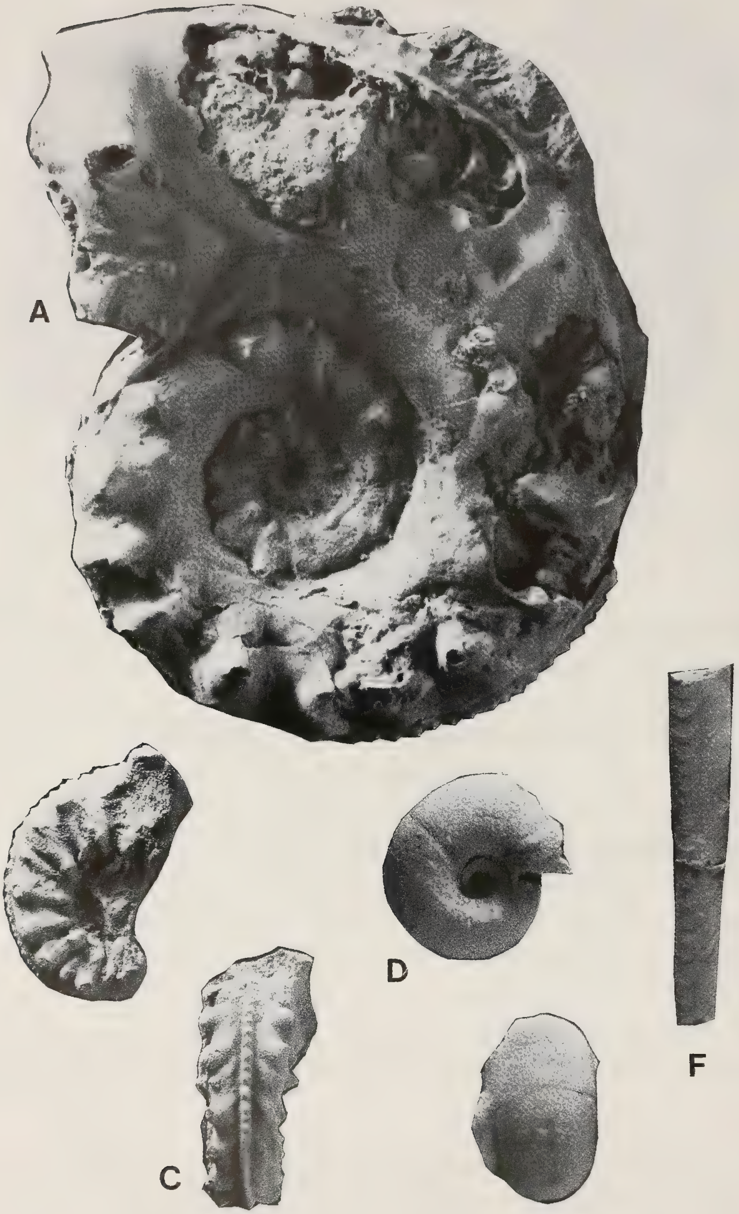

Figure 9

A. *Prionocycloceras* sp. × 1. Lateral view of SAM–PCA1775. B–C. *Prionocycloceras carvalhoi* (Howarth). × 1. Lateral and ventral views of SAM–PCA1758. D–E. *Tongoboryceras*? sp. juv. × 2. Lateral and ventral views of SAM–PCA1762. F. *Baculites klingeri* sp. nov. × 1. Lateral view of SAM–PCA1808.

P. corrugatus (Stanton) (Cobban & Scott, 1973: 45, pl. 18 (figs 6–19), fig. 17) and *P. matsumotoi* (Collignon) (1967: 47, pl. 28 (figs 3–4)) at similar growth stage. As noted by Cobban & Scott (1973), the specimen of *Diplomoceras*? *cascadense* Anderson figured by Basse (1963: 874, pl. 23 (fig. 4)), from the Upper Turonian of Angola, may be *P. corrugatus*.

The *Scalarites* sp. indet. of Collignon (1967, pl. 18 (fig. 2)) is too fragmentary for adequate comparison, but may belong here. So too may the *Glyptoxoceras* cf. *indicum* (Forbes) of Renz (1982: 73, pl. 22 (figs 7–8)) from the Early Turonian of Venezuela.

Stratigraphical occurrence

Currently, *Puebloites greenhornensis* Cobban & Scott is known only from the Lower Turonian of the Western Interior of North America, and the upper Middle Turonian of Angola. However, it may be present also in Venezuela and Morocco.

Superfamily BACULITACEAE Gill, 1871
Family **Baculitidae** Gill, 1871
Genus *Baculites* Lamarck, 1799

Type species

Baculites vertebralis Lamarck, 1801; by subsequent designation (Meek, 1876: 391).

Baculites klingeri sp. nov.

Figs 9F, 10, 11E–F

Diagnosis

A species of *Baculites* characterized by relatively strong ornament beyond a whorl height of about 5 mm. This comprises 2–4, variably developed, crescentic, dorsolateral bullae in a distance equal to the whorl height and projected growth striae on the upper flank. In some, weak flat-topped ribs cross the venter.

Types

SAM–PCA1737 is designated holotype. Paratypes are SAM–PCA1733–34, 1736, 1738, 1740–3, 1745, 1761, 1781, 1783, 1785, 1788, 1800, 1808 and 1833. All are from Bed V and all preserve recrystallized test; additional paratypes are SAM–PCA1731–32, 1737, 1739, 1744, 1747–49, 1751, 1757–60, 1763–66, 1768, 1770, 1773–74, 1779–80, 1782, 1784, 1786–87, 1788, 1790–91, 1793, 1797, 1799, 1801–6, 1809–13, 1815, 1817, 1819–20, 1823, 1825–26, 1830–31, 1835, 1837–38, 1840, 1842–43, 1847, 1849 and 1851.

Etymology

For Dr H. C. Klinger, in recognition of his important contribution to ammonite systematics in general, and an understanding of the Baculitaceae in particular.

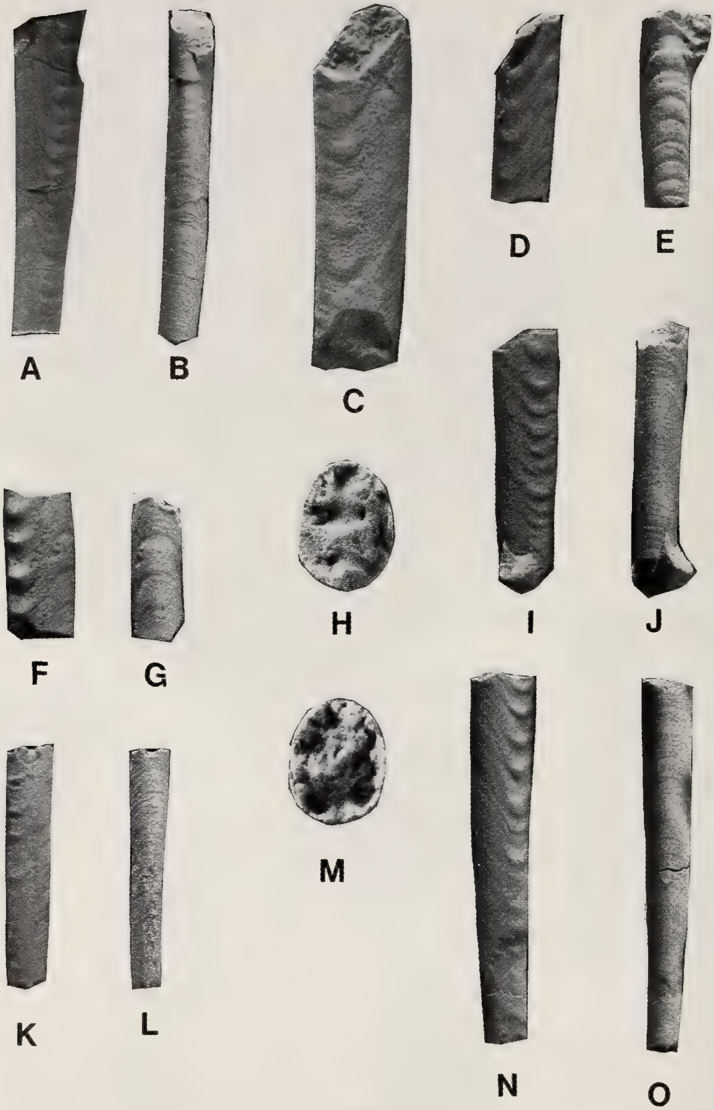

Figure 10

Baculites klingeri sp. nov. A–B. Lateral and ventral views of SAM–PCA1743. C. Lateral view of SAM–PCA1742. D–E. Lateral and ventral views of SAM–PCA1800. F–G. Lateral and ventral views of SAM–PCA1833. H. Whorl section of SAM–PCA1733. × 2. I–J. Lateral and ventral views of SAM–PCA1740. K–L. Lateral and ventral views of SAM–PCA1736. M. Whorl section SAM–PCA1788. × 2. N–O. Lateral and ventral view of the holotype, SAM–PCA–1737. All × 1 unless stated otherwise.

Description

Shell relatively small (maximum height = 9.5 mm), straight, tapering gradually adapically, with a compressed elliptical to weakly subovate whorl section (H/W = 1.17–1.39). The dorsum is evenly rounded and the relatively flat flanks converge slightly to the evenly rounded venter. Maximum width is at or just below midflank.

The earliest growth stages are smooth and the diameter at which tubercles first appear is variable. SAM–PCA1733 lacks flank tubercles at a whorl height of 7 mm, whereas in SAM–PCA1808 they are present at only 5.4 mm whorl height. Typically, the lower flanks are ornamented with 2–4 crescentic bullae of variable strength in a distance equal to the whorl height. In some individuals, e.g. SAM–PCA1833, these are swollen and form nodes (Fig. 10F). The upper flanks are ornamented with projected growth striae that recurve to cross the venter transversely, accompanied by weak, low, indistinct ribs that are broader than the interspaces. On SAM–PCA1800 there are five such ribs in a distance equal to twice the whorl height (Fig. 10D–E); they are much broader than the interspaces. The dorsum is ornamented only by transverse growth striae. Suture not observed.

Measurements

Specimen	H	W	H/W
SAM–PCA1754	9.5	7.0	1.36
SAM–PCA1740	8.5	6.5	1.31
SAM–PCA1737 (holotype)	8.2	6.5	1.26
SAM–PCA1738	8.0	5.8	1.39
SAM–PCA1783	7.0	5.5	1.27
SAM–PCA1735	7.0	6.0	1.17

Discussion

The Angolan material is closest to *Baculites yokoyamai* Tokunaga & Shimizu (1926: 195, pl. 22 (fig. 5), pl. 26 (fig. 11); Matsumoto & Obata, 1963: 30, pl. 8 (fig. 5), pl. 10 (figs 1–6), pl. 11 (figs 1, 4–5), pl. 12 (fig. 3), pl. 14 (fig. 4), figs 72–87)) in whorl section and the angle of the ventral rostrum, i.e. the angle between the venter and the projected growth striae on the upper flank. In general, however, the Japanese material appears to have much weaker ornament; so too does *B. besairiei* Collignon (1931: 37, pl. 5 (figs 6–9), pl. 9 (fig. 16)), *B. roedereri* Collignon (1931: 38, pl. 5 (fig. 10), pl. 9 (fig. 7)), and *B. latelobatus* Collignon (1931: 38, pl. 5 (figs 11–12), pl. 9 (fig. 18)) from the Upper Coniacian of Mahagaga (Madagascar); Klinger & Kennedy (1996) include the three Madagascan species in the synonymy of *B. yokoyamai*.

In ornament and small size, the Angolan material is close to *B. mariasensis* Cobban (1951: 818, pl. 118 (figs 10–12), text-figs 4–7; Kennedy & Cobban 1991: 69, pl. 13 (figs 11–16, 22–23, 29–33, 38–40), pl. 14 (figs 1–23, 26–28, 43–48), text-fig. 25E). The latter however is a younger Middle Coniacian to Middle Santonian species with distinctly ovoid to pyriform whorl section. Upper Turonian *B. undulatus* Roman & Mazeran

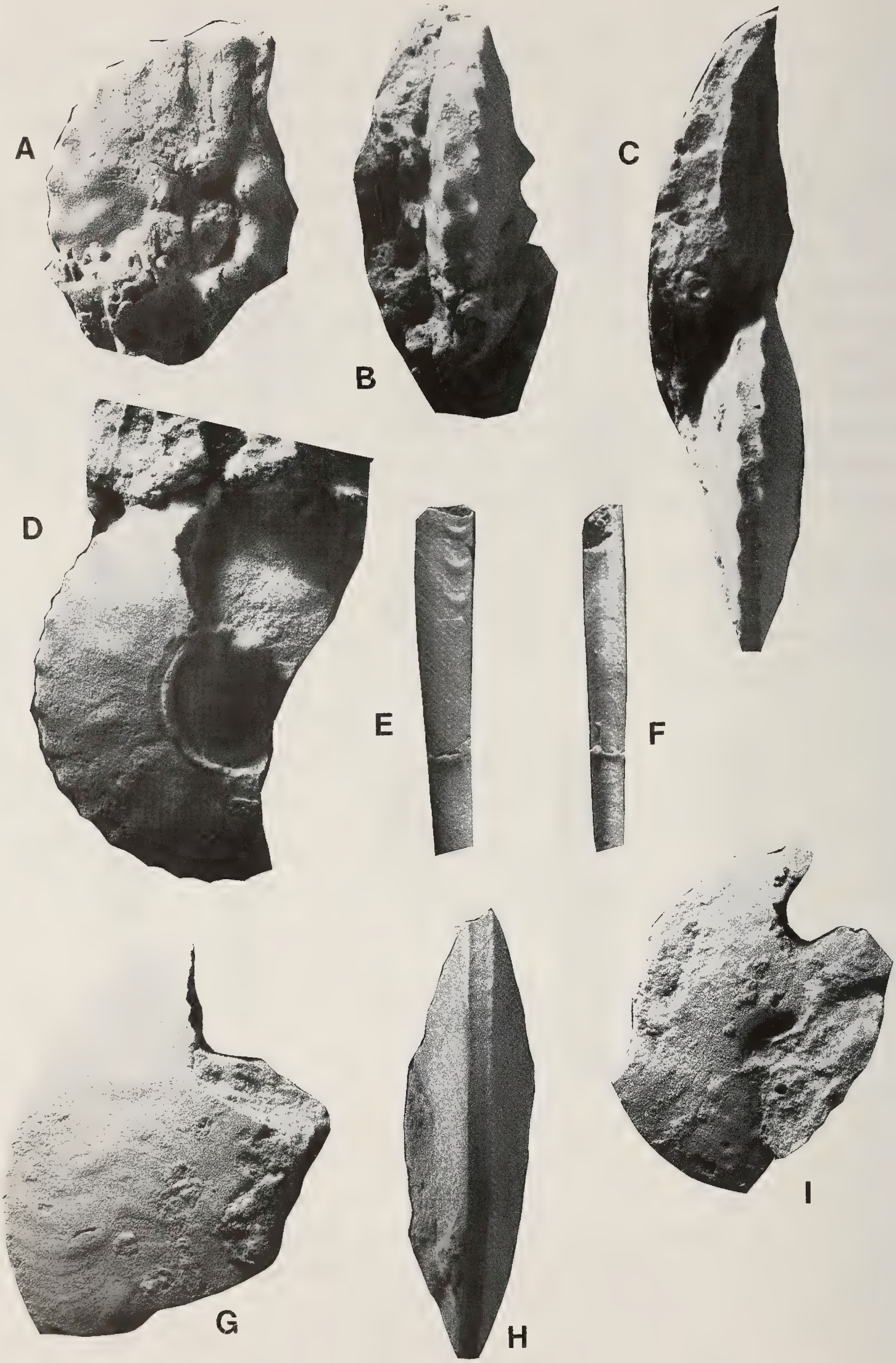

Figure 11

(1913: 11, pl. 4 (figs 6–8); Matsumoto & Obata 1963: 28, pl. 8 (fig. 4), pl. 9 (figs 1–5), pl. 11 (figs 2–3), text-figs 62–71) has a more ovate whorl section, with weaker tubercles and finer, denser, better developed ribs.

Baculites schenki Matsumoto (1959: 113, pl. 32 (figs 1–6), figs 12–25; Matsumoto & Obata, 1963: 38, pl. 12 (figs 1–2), pl. 14 (fig. 1), text-figs 90, 131–33) is allied to *B. klingeri* sp. nov., but has a more ovate whorl section, as has *Baculites boulei* Collignon (1931: 35, pl. 5 (fig. 2), pl. 9 (fig. 14); Matsumoto & Obata, 1963: 43, pl. 13 (figs 3, 5), pl. 15 (fig. 6), figs 93, 152–55); the latter species also has stronger more distant tubercules and is regarded a synonym of *B. capensis* Woods (Klinger & Kennedy 1996).

Baculites brevicosta Schlüter (1872: 141, pl. 39 (figs 9–10)) resembles the present form but has a subtrigonal whorl section and narrower venter, with 5 fine ribs in a distance equal to the whorl height.

Stratigraphical occurrence

Baculites klingeri sp. nov. is known only from the Lower Coniacian of Angola.

Order AMMONITIDA Hyatt, 1889
Suborder HOPLITINA Spath, 1922
(*nom. transl.* Cooper 1992 *ex* Hoplitida Spath, 1922)
Superfamily DESMOCERATACEAE Zittel, 1895
Family **Desmoceratidae** Zittel, 1895
Genus *Damesites* Matsumoto, 1942*a*

Type species

Desmoceras damesi Jimbo, 1894; by original designation (Matsumoto, 1942*a*: 24).

Damesites ainuanus Matsumoto, 1957
Figs 3C–D, 5H

1957 *Damesites ainuanus* Matsumoto, p. 86, pl. 15 (figs 1–2).
1968 *Damesites ainuanus* Matsumoto; Howarth, p. 6, pl. 1 (figs 3–5).

Material

A single fragmentary specimen, SAM–PCA1756 from Bed V, preserving recrystallized test.

Fig. 11. (*see facing page*). A–D, G–I. *Placenticeras kaffrarium* Etheridge. A–D. *Kaffrarium* morphotypes. A–B. Lateral and ventral views of SAM–PCA1905. C–D. Ventral and lateral views of SAM–PCA1730. G–I. *Umkwelanense* morphotypes. G–H. Lateral and ventral views of SAM–PCA1726. I. Lateral view of SAM–PCA1727. E–F. *Baculites klingeri* sp. nov. Lateral and ventral views of SAM–PCA1733. All × 1.

Description

The shell is very involute and compressed, with a tiny deep umbilicus (10% of the diameter) which has steep walls and evenly rounded shoulders. The flanks are almost flat, with maximum width at about midflank, and the whorl section is oval compressed (H/W = 1.25). The evenly rounded venter shows a very weak, low siphonal keel. The test is smooth and lacks ornament.

Measurements

Specimen	D	H	W	H/W	U
SAM–PCA1756	21	12.5 (59)	10 (48)	1.25	2 (10)

Discussion

Differences between *D. ainuanus* and other *Damesites* species have been covered by Matsumoto (1957) and Howarth (1968).

Stratigraphical occurrence

Damesites ainuanus Matsumoto is known from the Upper Turonian of Japan and the Lower Coniacian of Angola.

Family **Pachydiscidae** Spath, 1922
Genus *Tongoboryceras* Houša, 1967

Type species

Lewesiceras tongoboryense Collignon, 1952; by original designation (Houša, 1967: 42).

Tongoboryceras? sp. juv.
Fig. 9D–E

Material

Two juvenile specimens, SAM–PCA1762 and 1767, both from Bed V and both preserving recrystallized test.

Description

The shell is inflated and moderately evolute, with about 65 per cent of the preceding whorl covered. The umbilicus is rather narrow (about 25 per cent of the shell diameter), deep, with steep walls which pass imperceptibly into strongly convex flanks. The venter is broadly rounded and the semi-circular whorl section depressed (H/W = 0.74). Ornament is lacking but there is a distinct umbilical bulla on the adoral part of SAM–PCA1762, with a weaker one half a whorl behind. A conspicuous prorsiradiate constriction is adorally convex across the flanks, and forms a weak, anteriorly directed chevron across the venter.

Measurements

Specimen	D	H	W	H/W	U
SAM–PCA1762	11.8	5.1 (43)	6.9 (58)	0.74	3.0 (25)

Discussion

The available specimens are too small to be certain of generic identity. However, their weak ornament and strongly convex flanks suggest reference to Houša's (1967) genus.

Stratigraphical occurrence

Tongoboryceras is an Upper Turonian to Coniacian genus known from southern England, France, Madagascar, and Zululand; the Angolan specimens are from the Lower Coniacian.

Superfamily PUZOSIACEAE Spath, 1922
(*nom. transl.* Cooper & Greyling 1996 *ex* Puzosiidae Spath, 1922)

Family **Puzosiidae** Spath, 1922

Genus *Mesopuzosia* Matsumoto, 1954

Type species

Mesopuzosia pacifica Matsumoto, 1954; by original designation (Matsumoto, 1954: 79).

Mesopuzosia indopacifica (Kossmat, 1898)
Figs 12–13

1898	*Puzosia indopacifica* Kossmat, p. 117, pl. 17 (fig. 2a, b).
non 1932	*Puzosia (Parapuzosia) indopacifica* (Kossmat); Collignon, p. 18, pl. 6 (fig. 1a, b).
1954	*Mesopuzosia indopacifica* (Kossmat); Matsumoto, p. 84.
1958	*Puzosia (Parapuzosia) hearni* Anderson, p. 238, pl. 38 (fig. 1a, b).
1959	*Mesopuzosia indopacifica* (Kossmat); Matsumoto, p. 19.
?1961	*Puzosia eboroensis* Collignon, p. 34, fig. 1.
?1961	*Puzosia orientalis* (Matsumoto); Collignon, p. 32, pl. 5 (fig. 1).
?1967	*Mesopuzosia* aff. *indopacifica* (Kossmat); Jones, p. 41, pl. 4 (figs 30–35).
1988	*Mesopuzosia indopacifica* (Kossmat); Matsumoto & Kera (*in* Matsumoto), 1988: 76, figs 28–30.

Material

A single specimen, SAM–PCA1852, retaining recrystallized test.

Description

The shell is moderately large, compressed, and rather evolute, with slightly less than half the preceding whorl covered. The umbilicus is fairly wide (30–32 per cent of the

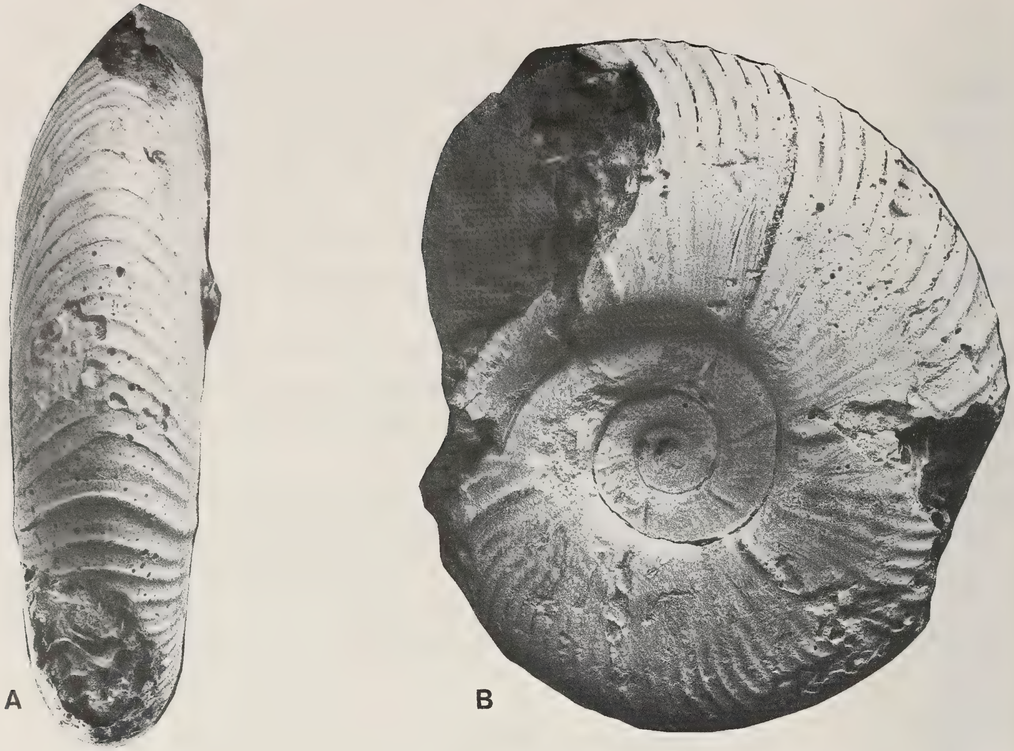

Figure 12

Mesopuzosia indopacifica (Kossmat). × 0.75. (A) Ventral and (B) lateral views of SAM–PCA1852.

diameter), with steep umbilical walls and subrounded shoulders. The broad flattish flanks converge slightly to the narrow, evenly rounded venter giving a compressed, oval whorl section (H/W = 1.25–1.42) (Fig. 13).

Ornament comprises seven prominent main ribs per whorl; these begin at the umbilical seam, are straight and slightly prorsiradiate across the flanks, and flex forwards slightly near the venter. Between main ribs are 10–13 long ribs that arise close to the umbilical shoulder and become prominent on the outer flank where they are joined by occasional short intercalatories.

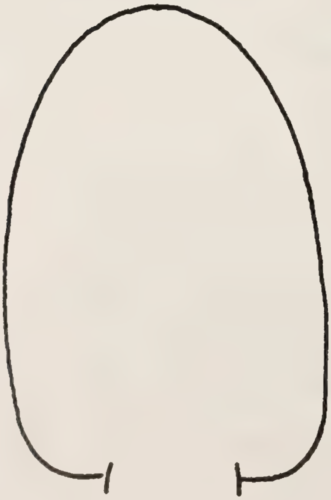

Figure 13

Mesopuzosia indopacifica (Kossmat). × 1. Whorl section of SAM–PCA 1852.

Measurements

Specimen	D	H	W	H/W	U
SAM–PCA1852	152	64 (42)	45 (30)	1.42	49 (32)
"	113	45 (40)	36 (32)	1.25	34 (30)

Discussion

Kossmat's (1898) figure differs from the Angolan example in having the main ribs more strongly projected across the venter, but this may be due to artistic licence. *Mesopuzosia eboroensis* (Collignon) (1961: 34, fig. 1) barely differs from the Angolan specimen and may be conspecific. Contemporary *Puzosia orientalis* Collignon (*non* Matsumoto) (1961: 32, pl. 5 (fig. 1)) is also very close to *M. indopacifica*, but has more (12–15) ribs between constrictions (main ribs).

Middle Turonian *Mesopuzosia pacifica* Matsumoto (1954: 82, pl. 14 (fig. 1), pl. 15 (figs 1–2), pl. 16 (figs 1–3), text–fig. 2; Matsumoto *et al.* (*in* Matsumoto), 1988: 46, figs 8–11, 25B–D) is separated from *M. indopacifica* by its more inflated whorls, convex flanks and more flexed ribs. Although the differences seem slight (*cf.* Jones 1967), they appear to be consistent.

Mesopuzosia beloensis Collignon (1965: 4, pl. 377 (fig. 1638)) is an Upper Turonian species seemingly intermediate between *M. ambikyensis* Collignon and *M. pacifica* Matsumoto. It is more involute (umbilicus 27 per cent of the diameter) than the Angolan specimen, as is *M. ambikyensis* Collignon (1965: 20, pl. 421 (fig. 1749)) which, in addition, is more compressed and with fewer (5–6) sinuous constrictions.

Coniacian *Mesopuzosia yubarensis* (Jimbo) (1894: 28, pl. 1 (fig. 6); Matsumoto *et al.* (*in* Matsumoto), 1988: 68, figs 21–24, 25F, 26–27) differs from *M. indopacifica* in having finer, more numerous ribs, as does *M. manasoaensis* (Collignon) (1961: 34, pl. 5 (fig. 2)). According to Matsumoto (1988), Howarth's (1968: 5, pl. 2 (figs 1–2)) specimen of *M. yubarensis* from Ponta Grossa is a juvenile *Pachydesmoceras*.

Mesopuzosia takahashii Matsumoto (1988: 52, figs 12–18, 25E) is a densely ribbed species which is unlikely to be confused with the present form.

Stratigraphical occurrence

Typically *Mesopuzosia indopacifica* (Kossmat) is a Middle Turonian to Coniacian species known from California, Japan, India, Madagascar, Zululand and Angola.

Subfamily Hauericeratinae de Grossouvre, 1894

Discussion

Matsumoto *et al.* (1990) provide the most recent comment on the status and composition of the subfamily; an origin is sought in *Puzosia*, via keeled *'Puzosia' serratocarinata* Kennedy & Cobban (1988: 595, figs 2, 4.1–3).

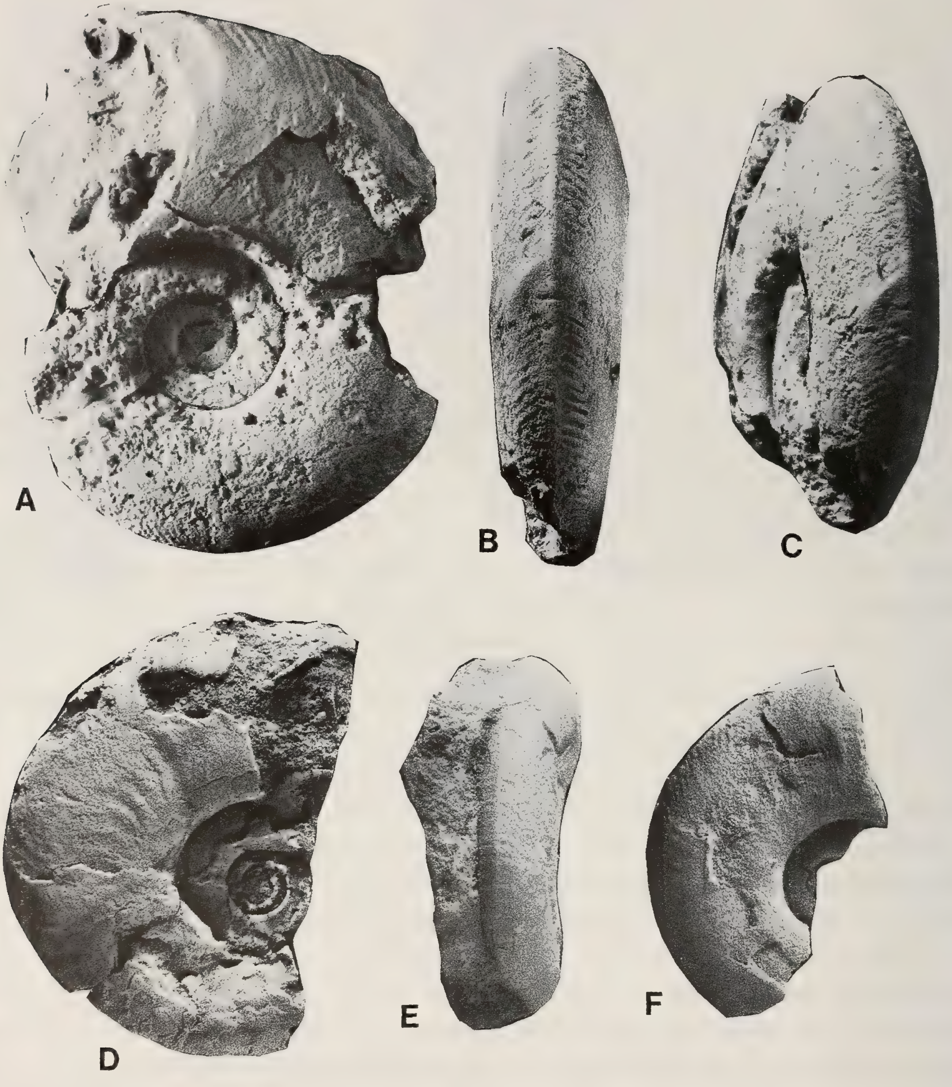

Figure 14

Mossamedites serratocarinatus (Kennedy & Cobban). A–C. Lateral, ventral and oblique ventral views of SAM–PCA1853. × 1. D. Lateral view of SAM–PCA1860. × 1.5. E–F. Ventral and lateral views of SAM–PCA1876. × 1.5.

Genus *Mossamedites* gen. nov.

Type species

Puzosia serratocarinata Kennedy & Cobban, 1988; by original designation herein.

Discussion

Mossamedites provides the link between evolute and moderately inflated *Puzosia*, e.g. *P. compressa* Kossmat, and very evolute and compressed *Hauericeras* of the Santonian, with a conspicuously raised siphonal keel. It retains the ornament and suture of *Puzosia* and has the shell form of *Hauericeras*; the sharpened venter of *Mossamedites* represents an intermediate stage between the rounded venter of *Puzosia* and the specialized keel of mature *Hauericeras*.

The type species of *H. (Hauericeras)*, viz. *H. pseudogardeni* (Schlüter) (Matsumoto *et al.*, 1990: 440, fig. 1) differs from *Mossamedites* gen. nov. in being more compressed, with a distinctly raised keel to the venter, weaker ventral ribs, and in possessing ventrolateral nodes, a shallow spiral groove on the upper flank, constrictions that are adorally biconcave, and gradually descending auxiliary lobes. *Hauericeras (Gardeniceras) gardeni* (Baily) (Matsumoto & Obata 1955: 139) differs from *Mossamedites* gen. nov. in being more compressed, more evolute, with a very different siphonal keel, and without trace of tubercles or ribs.

Mossamedites serratocarinatus (Kennedy & Cobban, 1988)
Fig. 5G, 14

1972	*Hauericeras* sp.; Cooper, p. 248.
1988	*Puzosia serratocarinatus* Kennedy & Cobban, p. 595, figs 2, 4: 1–3.

Material

This is a fairly common species in the Angolan fauna, and is represented by ten more or less fragmentary specimens from Bed IV, all of which preserve recrystallized test; SAM–PCA1853, SAM–PCA1855–56, 1858, 1860–1862, 1865, 1876 and 1883.

Description

The shell is strongly compressed and moderately evolute, with slightly less than half the preceding whorl covered. The umbilicus is wide (25–33% of the diameter) and shallow, with vertical walls and subrounded shoulders. The broad, weakly convex flanks curve to the narrow fastigiate venter, resulting in a compressed, sublanceolate whorl section (H/W = 1.45–1.56). The venter is sharpened along the siphonal line but there are no bounding sulci and only the lowest of siphonal keels.

On the early whorls ornament comprises sinuous, prorsiradiate growth striae that flex forwards near the venter and are followed, e.g. SAM–PCA1876, by an occasional weak collar that probably marks a constriction on the internal mould. Beyond about 30 mm diameter the ribs strengthen and are restricted to the ventral region, forming obtuse chevrons at the siphonal line and weakly serrating the low keel. These dense prorsiradiate ribs are about as wide as the interspaces, with 13 in a 15 mm distance at 50 mm diameter. Constrictions are lacking but periodic low collars across the venter probably mark their position on the internal mould.

Measurements

Specimen	D	H	W	H/W	U
SAM–PCA1853	*c.* 72	30 (*c.* 42)	?	?	22 (*c.* 31)
"	44	17 (*c.* 39)	12 (*c.* 27)	1.42	11 (*c.* 25)
SAM–PCA1862	*c.* 54	24 (*c.* 44)	15 (*c.* 28)	1.60	18 (*c.* 33)
"	44	20 (45)	13 (*c.* 30)	1.54	14.5 (*c.* 33)

Discussion

The present material differs from the fragmentary type material from the upper Middle Turonian of northern Mexico in being more involute (umbilicus 25–33 vs. 37 per cent of the diameter) and somewhat more compressed (H/W = 1.42–1.56 vs. 1.61–1.70). However given the small amount of material currently available the differences, probably, are not taxonomically meaningful.

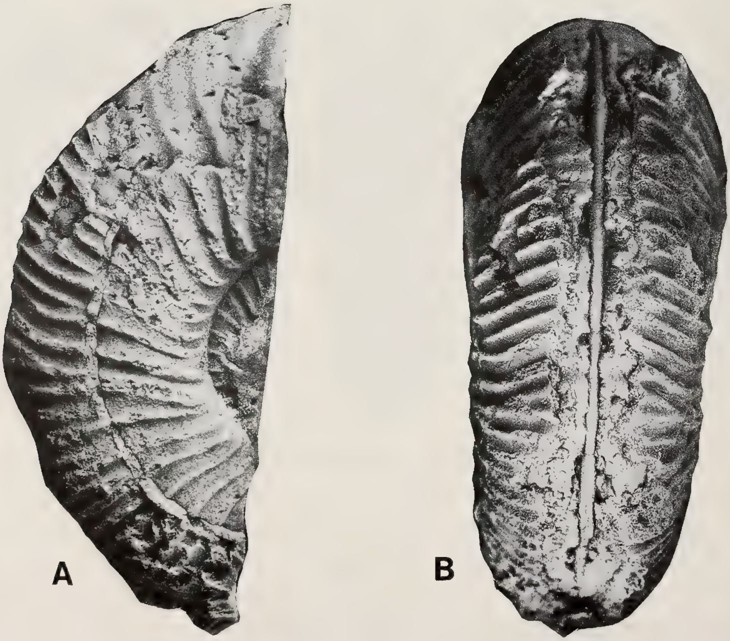

Figure 15

Kossmaticeras (Kossmaticeras) theobaldianum theobaldianum (Stoliczka). × 1.5. Lateral and ventral views of SAM–PCA1902.

The Angolan material closely resembles (and probably is ancestral to) Lower Coniacian *Hauericeras antiquum* Collignon (1961: 75, fig. 12) but the latter species is more evolute (umbilicus 40 per cent of the shell diameter), as is the ribbed *Hauericeras* aff. *gardeni* (Baily) of Renz (1982: 106, pl. 35 (fig. 2)) from the Upper Coniacian or Santonian of Venezuela.

Stratigraphical occurrence

Mossamedites serratocarinatus (Kennedy & Cobban) is known only from the upper Middle Turonian of northern Mexico and Angola.

Family **Kossmaticeratidae** Spath, 1922
Subfamily Kossmaticeratinae Spath, 1922
Genus *Kossmaticeras* de Grossouvre, 1901

Type species

Ammonites theobaldianus Stoliczka, 1865; by original designation (De Grossouvre, 1901: 719).

Kossmaticeras theobaldianum (Stoliczka, 1865)
Fig. 15

1865	*Ammonites theobaldianus* Stoliczka, p. 161, pl. 78 (figs 2–3).
1897	*Holcodiscus theobaldianus* (Stoliczka); Kossmat, p. 142, pl. 18 (figs 4–5a, b), pl. 19 (fig. 1a, b).
1906	*Holcodiscus theobaldianus* (Stoliczka); Boule *et al.*, p. 25, pl. 7 (figs 2–3).
1955	*Kossmaticeras theobaldi* (Stoliczka); Collignon, p. 20, pl. 1 (figs 2–3), pl. 2 (fig. 1) (*cum synon.*).
1985	*Kossmaticeras (Kossmaticeras) theobaldianum theobaldianum* (Stoliczka); Kennedy & Klinger, p. 170, figs 2A–E only (?*non* 1D–E = *K. recurrens* (Kossmat)) (*cum synon.*).

Material

A single fragmentary specimen, SAM–PCA1902 from Bed VI, preserving recrystallized test.

Description

The shell is moderately evolute, compressed, with about half the preceding whorl covered. The umbilicus is fairly wide (35 per cent of the diameter), with vertical walls and well-rounded shoulders. The somewhat flattened flanks converge slightly to the broadly rounded venter and the oval whorl section is as high as wide (H/W = 1.00).

Primary ribs begin at the umbilical seam and are rursiradiate to the umbilical shoulder, where they bend forwards to become prorsiradiate and weakly falcate across the flank. Ribs frequently bifurcate, or are separated by an intercalatory from the point of geniculation, so that twice as many ribs cross the venter as leave the umbilicus. There are about 35 ribs per half whorl across the venter. Since the outer whorl covers the preceding whorl to exactly the level of bifurcation and intercalation, all ribs in the umbilicus are simple. Periodic constrictions, each marked by a strengthened rib bearing a distinct umbilical bulla, cut across ribs to the posterior and parallel those to the anterior.

Measurements

Specimen	D	H	W	H/W	U
SAM–PCA1902	52	23 (44)	23 (44)	1.00	18 (35)

Discussion

The Angolan specimen closely resembles figured material of *K. theobaldianum* and comparison with other species is noted by Kennedy & Klinger (1985).

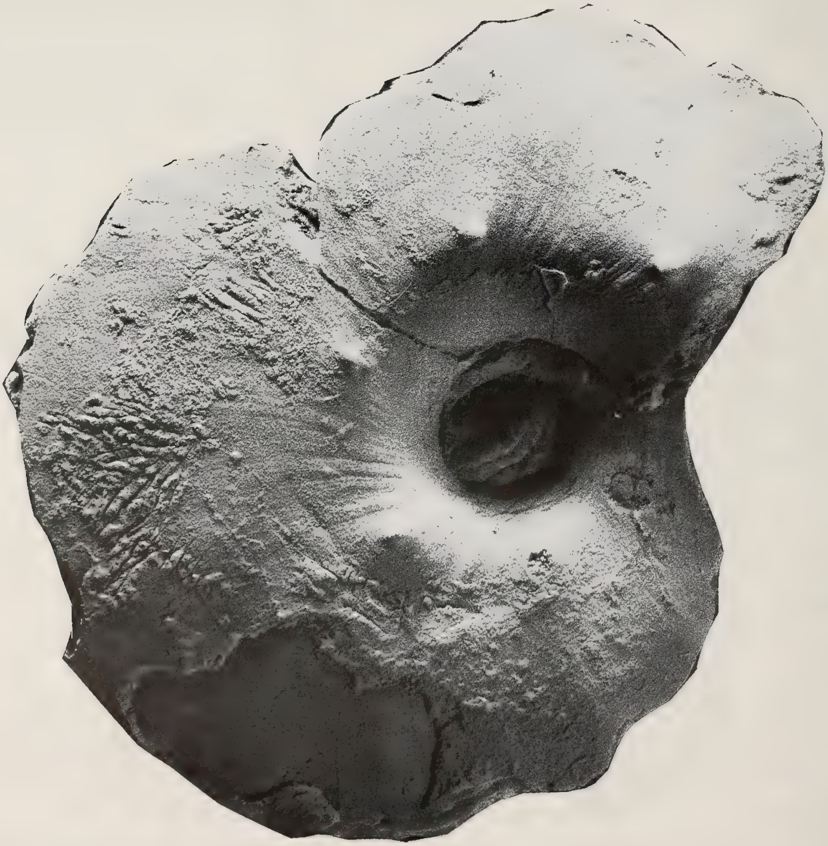

Figure 16

Placenticeras kaffrarium Etheridge. × 1. Lateral view of SAM–PCA1869.

Stratigraphical occurrence

Kossmaticeras theobaldianum (Stoliczka) is a typical Lower Coniacian species, apparently restricted to the Austral Realm. It is recorded from southern India, Madagascar, Zululand and now Angola.

Superfamily HOPLITACEAE Douvillé, 1890
Family **Placenticeratidae** Hyatt, 1900
Subfamily Placenticeratinae Hyatt, 1900
Genus *Placenticeras* Hyatt, 1900

Type species

Ammonites placenta DeKay, 1828; by the subsequent designation of Meek, 1876.

Placenticeras kaffrarium Etheridge, 1904
Figs 5I–J, 11A–D, G–I, 16

1904	*Placenticeras kaffrarium* Etheridge, p. 89, pl. 3 (fig. 16).
1978*b*	*Proplacenticeras kaffrarium* (Etheridge); Cooper, p. 6.
1989	*Placenticeras kaffrarium* Etheridge; Klinger & Kennedy, p. 268, figs 9–14A, 19–20, 22–99 (*cum synon.*).

Material

Seventeen specimens, wholly or partially retaining recrystallized test. Of these, 12 are *P. kaffrarium* morphotypes, SAM–PCA1869 is from Bed IV, SAM–PCA1730 and 1746 are from Bed V, and SAM–PCA1897, 1905, 1915, 1952–3, 1956, 1959, and 1962 are from Bed VI. Of the 5 *P. umkwelanense* morphotypes, SAM–PCA1726–7 and 1778 are from Bed V and SAM–PCA1954 and 1961 are from Bed VI.

Description

Placenticeras kaffrarium morphotype.

Shell typically placenticeratid, high-whorled, discoidal and very involute, with 90 per cent of the preceding whorl covered. The narrow funnel-like umbilicus (about 13 per cent of the shell diameter) has a steeply sloping, flat umbilical wall that grades into the subrounded shoulder. Broad, moderately convex flanks converge markedly to the narrow tabulate venter which is flanked by abrupt, angular ventrolateral shoulders. Maximum width is midway between the umbilical shoulder and midflank, and the degree of inflation varies from individual to individual. Due to allometric growth, the umbilical ratio increases with ontogeny, and the venter of macroconchs rounds in later growth.

Ornament comprises 6–7 small, acute umbilical tubercles per whorl and, on the outer flank, there are 12–14 variably developed, broad, low bulges. Alternate bulges correspond more or less closely with umbilical tubercles. The angular ventrolateral shoulders are ornamented by 24–26 small, distinct clavi per whorl which alternate across the venter in zigzag fashion.

Placenticeras umkwelanense morphotype

The shell is strongly compressed, discoidal, high-whorled, and involute. The narrow umbilicus (about 14 per cent of the shell diameter) has steep walls and subrounded shoulders. The broad flanks are weakly convex and converge markedly to the narrowly sulcate venter. In one juvenile (Fig. 11H) the venter is weakly raised along the siphonal line and thus pseudotricarinate. Umbilical tubercles and ventrolateral clavi are lacking. There are low falcate bulges on the outer flank, separated by falcate growth striae, but these are variably developed and lacking from the largest specimen, SAM–PCA1961.

Measurements

Specimen	D	H	W	H/W	U
SAM–PCA1727	*c.* 50	26 (52)	?	?	*c.* 7.0 (14)
SAM–PCA1726	*c.* 71	*c.* 38 (54)	*c.* 17.0 (45)	2.24	?
SAM–PCA1915	67	35 (52)	17.5 (26)	2.00	8.8 (13)

Discussion

As noted by Klinger & Kennedy (1989), *Placenticeras kaffrarium* Etheridge displays high intraspecific variability, manifest in the degree of inflation of the whorls, the prominence of the lateral bulges and umbilical tubercles, and the rounding of the venter. These features are sexually linked, with larger macroconchs being more inflated, with more conspicuous flank bulges and a broadly rounded venter at relatively early stage, when compared with the microconch.

Namibian *Placenticeras merenskyi* Haughton (1930: 363, pl. 11; Klinger 1977, fig. 7) differs from the present species in being more compressed, with smaller, more numerous umbilical (12) tubercles per whorl. Contrary to Howarth (1985) and Klinger & Kennedy

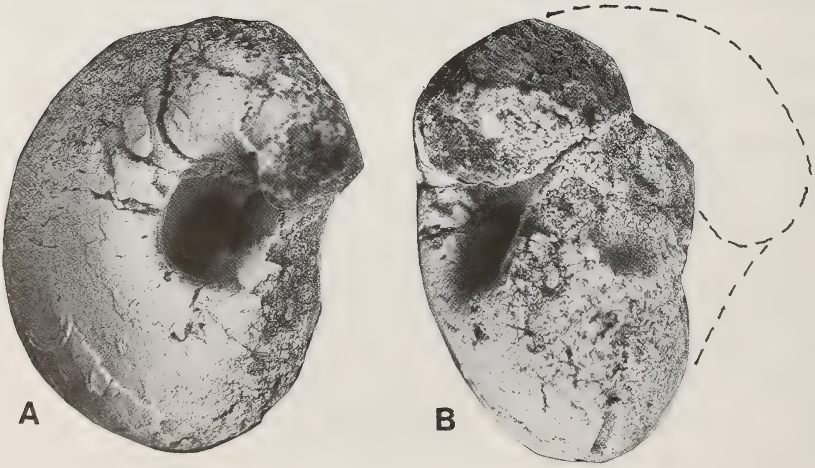

Figure 17

Vascoceras cf. *proprium* (Reyment). × 1.5. Lateral and anterior views of SAM–PCA1896.

(1989), the numerous small umbilical bullae exclude *P. merenskyi* from the present species and, the writer believes, it should fall into the synonymy of *P. memoria-schloenbachi* (Laube & Bruder) (1887: 221, pl. 23 (fig. 1)), an Upper Cenomanian–Turonian species.

Proplacenticeras fritschi (de Grossouvre 1894: 124, pl. 5 (figs 1–2)) from the Coniacian of La Ribochère, differs from *P. kaffrarium* in having ventrolateral clavi paired across the venter. Although most workers regard *Proplacenticeras* a subjective junior synonym of *Placenticeras*, in the context of hoplitacaean phylogeny the opposite ventrolateral clavi are phyletically and taxonomically meaningful and, here, *Proplacenticeras* is regarded a valid taxon.

Stratigraphical occurrence

Placenticeras kaffrarium Etheridge is a Middle Turonian–Coniacian species reported from Zululand, Madagascar, India, and Angola; in the latter region it occurs both in the upper Middle Turonian and Lower Coniacian, but only *P. kaffrarium* morphotypes are known from the lower level.

Suborder ACANTHOCERATINA Hyatt, 1900
(*nom. transl.* Cooper 1991 *ex* Acanthoceratida Hyatt, 1900)
Superfamily ACANTHOCERATACEAE de Grossouvre, 1894
Family **Vascoceratidae** Douvillé, 1912
Genus *Vascoceras* Choffat, 1898

Type species

Vascoceras gamai Choffat, 1898; by the subsequent designation of Diener, 1925: 182.

Vascoceras cf. *proprium* (Reyment, 1954)
Fig. 17

Compare:

1954	*Pachyvascoceras proprium* Reyment, p. 258, pl. 5 (fig. 1), fig. 3d.
1972	*Subtissotia*? sp.; Cooper, p. 248.
1987	*Vascoceras proprium* (Reyment); Kennedy *et al.*, p. 46, pl. 4 (figs 1–15, 18–19), pls 5–6, figs 8A–C, 9 (*cum synon.*).

Material

A single specimen, SAM–PCA1891 from Bed II, partially eroded but preserving recrystallized test.

Description

The shell is strongly inflated, globose, with a very narrow, crater-like umbilicus (about 15% of the diameter). The overhanging umbilical wall is broad, convex, with a well rounded shoulder. The convex flanks converge rather rapidly to the evenly rounded venter

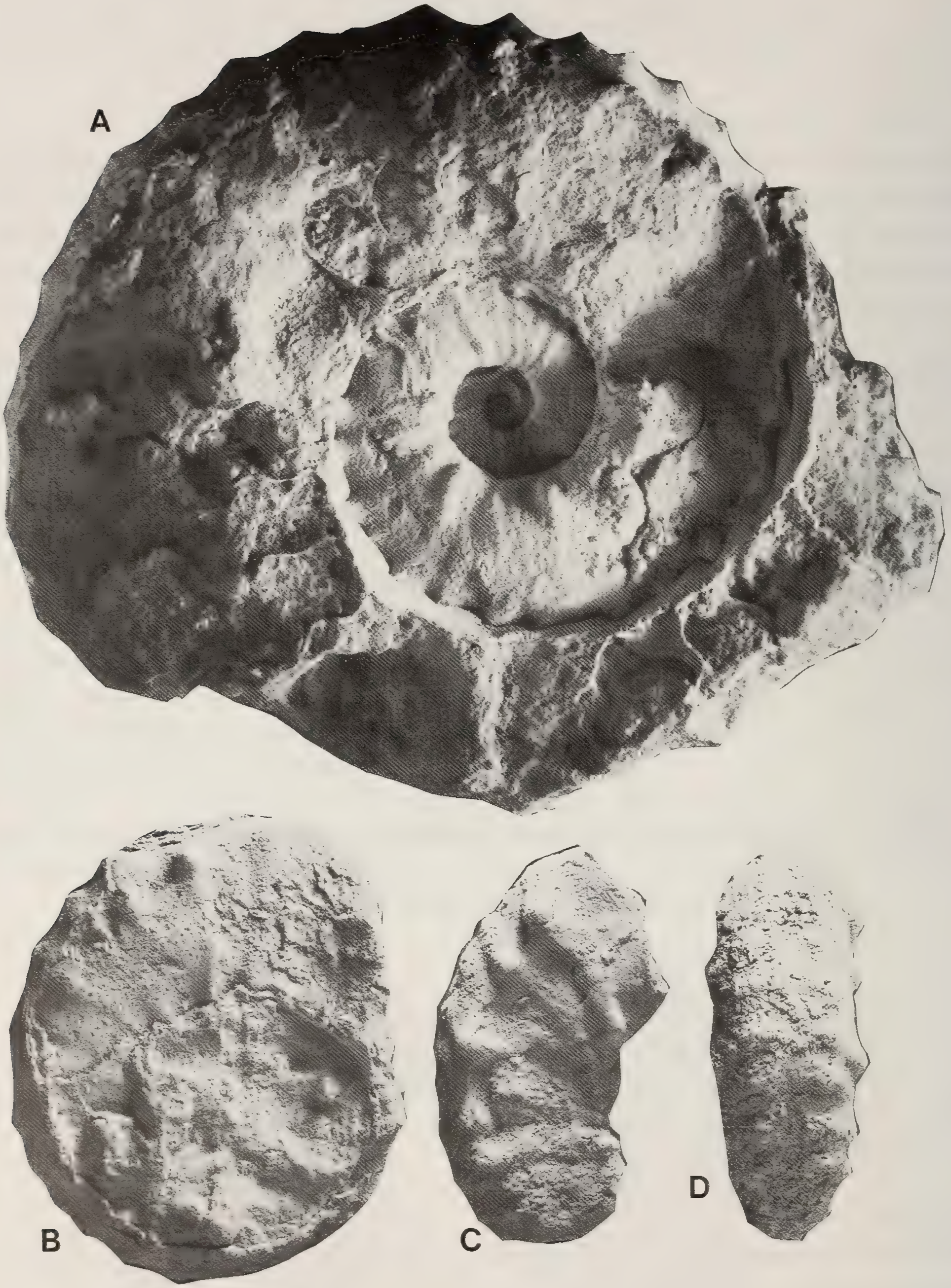

Figure 18

Morrowites mocamedensis (Howarth). × 1. A. Lateral view of SAM–PCA1892. B. Lateral view of SAM–PCA1887. C–D. Lateral and ventral views of SAM–PCA1889.

to produce a subtrigonal whorl section. Ornament is lacking and the suture is not displayed. Slight deformation and erosion make morphometric analysis unreliable and measurements are excluded.

Discussion

Although poorly preserved, the Angolan example shows all the essential features of Reyment's (1954) species. Given the wide range of variation admitted for *V. proprium* (*cf.* Kennedy *et al.* 1987), it may prove to be a subjective junior synonym of Tunisian *V. fleuryi* (Pervinquière).

Vascoceras hartti (Hyatt) (1870: 386; 1903: 103, pl. 14 (fig. 16); White 1887: 226, pl. 19 (figs 1–2), pl. 20 (fig. 3); Chancellor 1982: 98, figs 28C, 29–33) resembles the present specimen, especially in its subtrigonal whorl section, but the Brazilian species has steeply sloping umbilical walls.

Vascoceras kossmati Choffat (Berthou *et al.* 1985: 76, pl. 5 (figs 1–9)) (= *V. harttiforme* Choffat) resembles the Angolan specimen but has umbilical tubercles, a less undercut umbilical wall, and a broader rounder venter.

Stratigraphical occurrence

Vascoceras proprium (Reyment) is known with certainty only from the Lower Turonian of Texas, northern Mexico, Nigeria and probably Angola.

Family **Euomphaloceratidae** Cooper, 1978
(*nom. transl.* Cooper 1997 *ex* Euomphaloceratinae Cooper, 1978)
Subfamily Euomphaloceratinae Cooper, 1978
Genus *Morrowites* Cobban & Hook, 1983

Type species

Mammites depressus Powell, 1963; by original designation of Cobban & Hook (1983: 9).

Morrowites mocamedensis (Howarth, 1968)
Figs 18–19, 20A, E, 21–24

1968	*Mammites mocamedensis* Howarth, p. 222, pl. 3.
1985	*Pseudaspidoceras mocamedense* (Howarth); Howarth, p. 98.

Material

Six specimens, SAM–PCA1885, 1887–9 and 1892–93 from Bed II, partially or wholly preserving recrystallized test.

Description

The shell is evolute, compressed, with about 20 per cent of the preceding whorl covered. The evolute umbilicus (about 35 per cent of the diameter) is relatively shallow, with steep, fairly broad walls and subrounded shoulders. The broad flat flanks converge

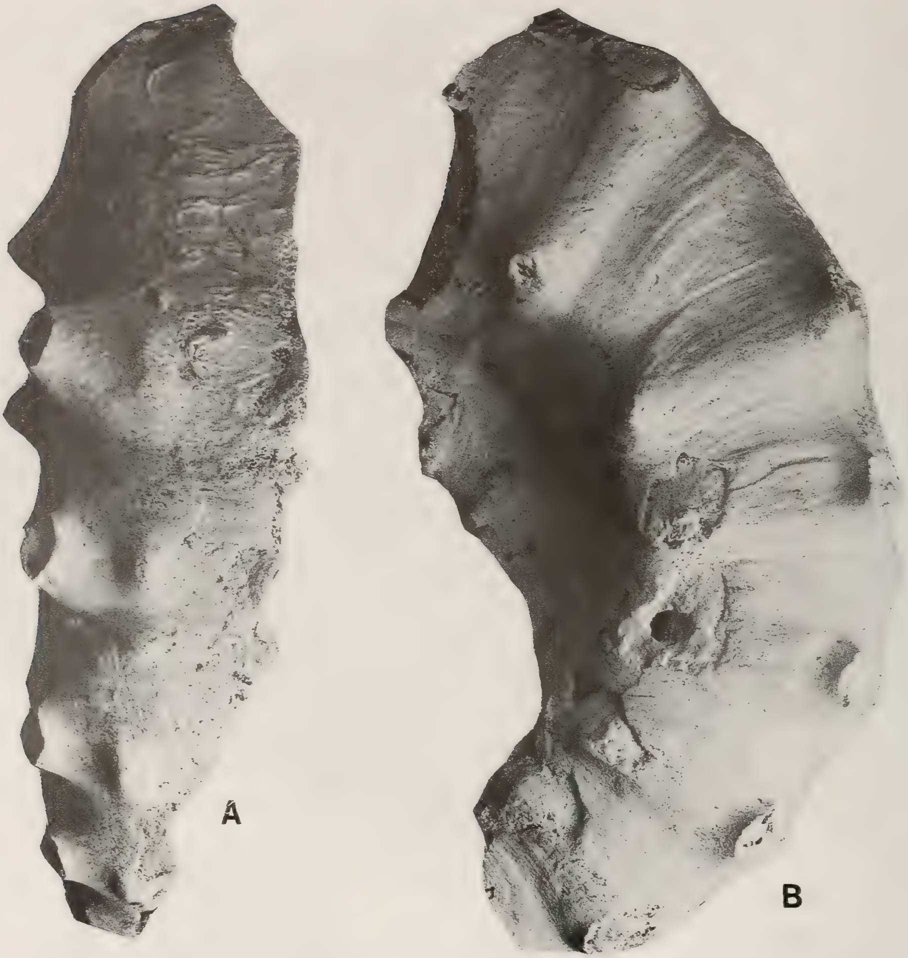

Figure 19

Morrowites mocamedensis (Howarth). × 0.66. Ventral and lateral views of SAM–PCA1885, a horned adult.

slightly toward the relatively broad, flattened venter. Costally the whorl section is polygonal, slightly higher than wide, with a weakly concave venter; intercostally it is broadly ovate and compressed (H/W = 1.09–1.32) (Fig. 20A, E), becoming more inflated with growth. Part of the poorly preserved suture is illustrated as Figure 30.

Ornament, especially the strength of tuberculation and ribbing, is variable. There are about 13 umbilical bullae per whorl on the best preserved specimen, but their strength varies and not all ribs develop bullae. Not uncommonly there is a weak arcuate bulla between main bullae, unconnected to a rib. The main umbilical bullae give rise to fairly thick low ribs. These are adorally convex across the flank, weak at midflank, and separated by up to three intercalatories. Main ribs are ornamented with inner and outer ventrolateral tubercles, although the latter tend to be irregular in strength and

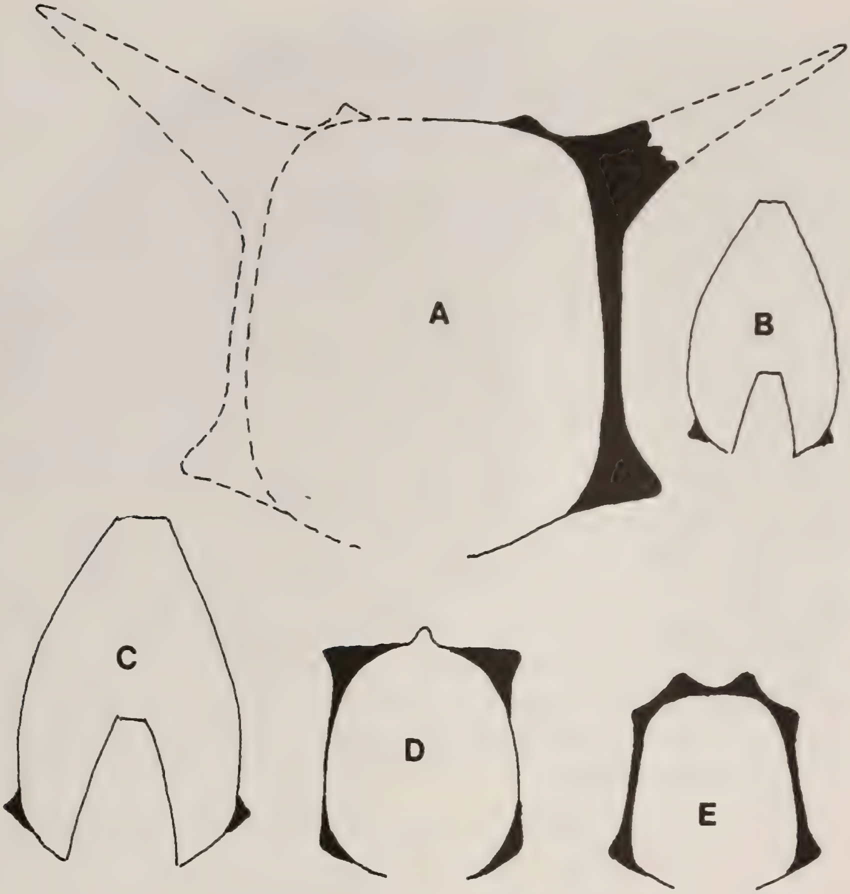

Figure 20

Whorl sections. × 1. A, E. *Morrowites mocamedensis* (Howarth). A. SAM–PCA1885; E. SAM–PCA1888. B–C. *Placenticeras kaffrarium* Etheridge. B. SAM–5106; C. SAM–6523. D. *Prionocycloceras carvalhoi* (Howarth). SAM–PCA1896.

development. From the inner ventrolateral tubercles the ribs project forwards to connect with outer ventrolateral tubercles close to the siphonal line and are weakly joined across the venter. There is a multiplicity of outer ventrolateral tubercles, unconnected to ribs, so that on SAM–PCA1892 15 outer ventrolateral tubercles correspond with only seven lower ventrolateral tubercles (Fig. 21). Occasionally an inner ventrolateral tubercle lacks an accompanying upper ventrolateral. That the inner ventrolateral tubercles represent the septate bases of hollow spines is evident from SAM–PCA1892; this specimen preserves 13 short, stubby, backwardly directed spines per half whorl impressed in the umbilical wall or the penultimate whorl.

SAM–PCA1885 represents this species in maturity, at a diameter of about 190 mm. It is compressed, evolute, with a wide, moderately deep umbilicus surrounded by broad, steeply inclined walls and evenly rounded shoulders. The broad flat flank converges

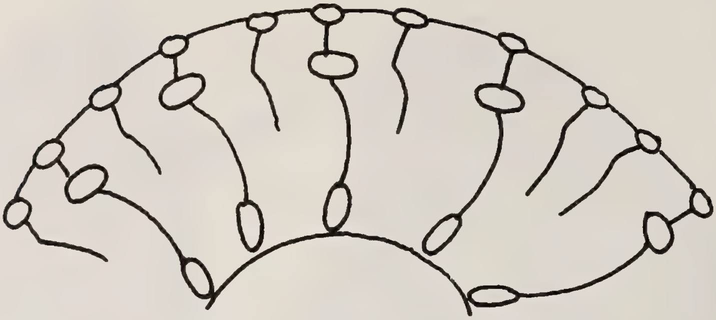

Figure 21

Morrowites mocamedensis (Howarth). Schematic rib pattern of SAM–PCA1888.

slightly to the weakly convex, flattened venter, and the costal whorl section is subquadrate, about as wide as high. Ornament comprises about eight prominent umbilical tubercles per half whorl. These give rise to coarse, distant, almost rectiradiate ribs that are narrower than the interspaces and ornamented by adorally convex growth striae. Ribs terminate at the ventrolateral shoulder in the swollen bases of hollow horns. At this growth stage intercalatories are lacking and ribbing does not cross the venter. There is a row of small nodate to weakly clavate outer ventrolateral tubercles, some of which occur in the interspaces between horns.

Measurements

Specimen	D	H	W	H/W	U
SAM–PCA1888	*c.* 100	*c.* 38 (38)	*c.* 35 (35)	1.09	35 (35)
"	72	27 (38)	24 (33)	1.13	25 (35)
SAM–PCA1892	105	43 (41)	*c.* 40 (38)	1.08	32 (30)

Discussion

The exaggerated ventrolateral horns of the present species preclude it from *Pseudaspidoceras* as currently interpreted. Although immature growth stages of the Angolan material conform closely to the type of *Pseudaspidoceras curvicostatum* Reyment (1955: 55, pl. 11 (fig. 1), pl. 12, text-fig. 24) and, initially, were identified as such, the outer whorls are *Mammites*-like, with exaggerated ventrolateral horns (Fig. 20A). Since ventrolateral horns are a feature of *Morrowites*, most emphasis is placed on these derived characters, and the Angolan material is assigned to Cobban & Hook's (1983) genus; unfortunately the character of the lateral lobe (L) could not be discerned in the Angolan material.

Zaborski (1995) included *Pseudaspidoceras curvicostatum* in the synonymy of *P. paganum* Reyment (1954: 253, pl. 4 (fig. 1), text-figs 3h, 4). Since the holotype of the

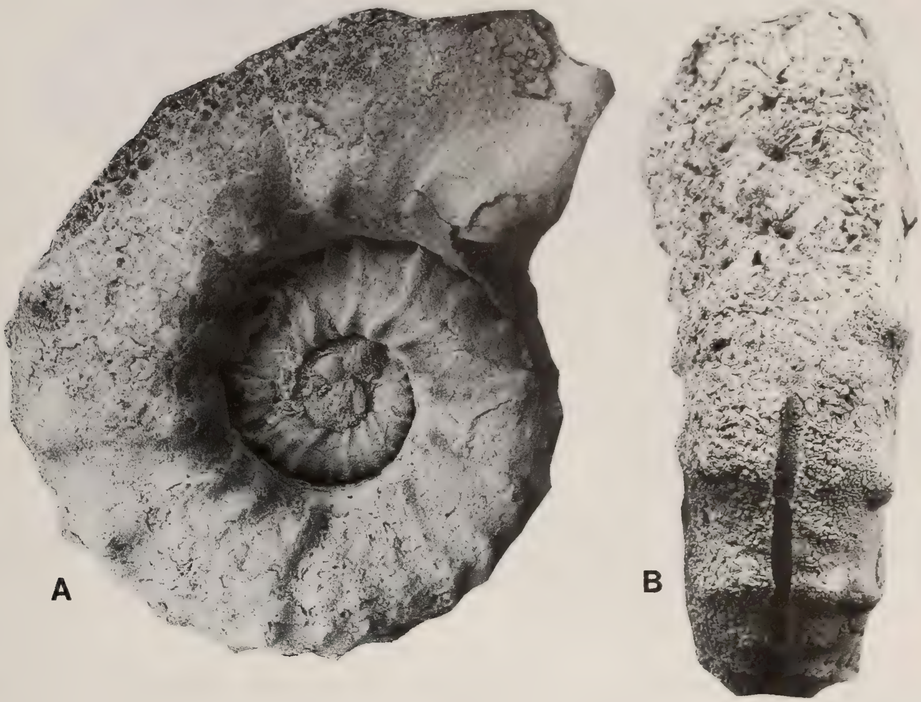

Figure 22

Morrowites mocamedensis (Howarth). × 1. Lateral and ventral views of SAM–PCA1888.

latter preserves body chamber at relatively small diameter and resembles a small *M. mocamedensis*, the two species could be dimorphs and synonyms; however, Zaborski (1995) does not report ventrolateral horns of the size seen in *M. mocamedensis* for *P. paganum*.

Morrowites depressus (Powell) (1963: 1228, pl. 168 (figs 1–3), pl. 170 (figs 4–5), pl. 171 (fig. 1), text-figs 5e, 6f–h; 1967: 313, figs 2–5) has much more-depressed whorls than the present species, with a wider venter and sparser more-rigid ribs to the inner whorls. *Morrowites subdepressus* Cobban & Hook (1983: 11, pl. 1 (figs 8–13), pl. 3 (figs 19–20), pl. 4 (figs 1–3, 12–16), pl. 7, text-figs 6–7) also has straighter, more-rigid ribs and, apparently, does not develop exaggerated ventrolateral horns.

Morrowites dixeyi (Reyment) (1955: 50, pl. 9 (fig. 4), pl. 11 (fig. 2), text-figs 20–21) does not develop the exaggerated ventrolateral horns of the present species; neither does *Morrowites michelobiensis* (Laube & Bruder) (1887: 231, unnumbered text figure on p. 231).

Pseudaspidoceras flexuosum Powell (Kennedy *et al.* 1987: 34, pl. 2 (figs 1–4, 8–13, 16–17), text-figs 3A–C, 5, 6C–D, 7A–C) differs from the present material in its subdued ornament, looped ribs across the venter, and lack of ventrolateral horns. It is said to include in its synonymy Madagascan *Ampakabites auriculatus* (Collignon) (1965: 29, pl. 388 (fig. 1662), pl. 389 (fig. 1664)) and *A. collignoni* Cobban & Scott (1973: 81, pl. 29

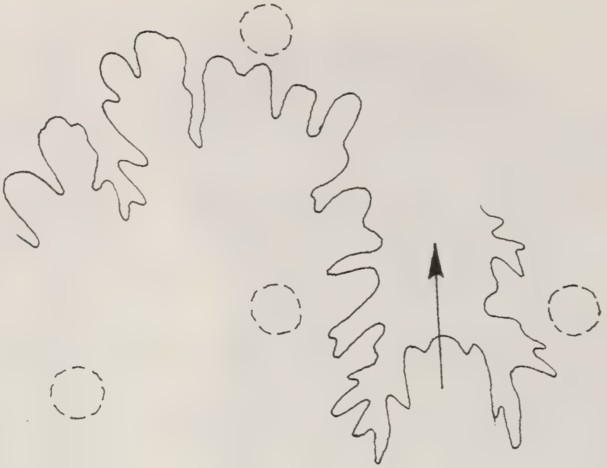

Figure 23

Morrowites mocamedensis (Howarth). Partial suture, showing external lobe (E) and lateral saddle (E/L), of SAM–PCA1892 at 85 mm diameter.

(figs 1–3), text-figs 39–40) from the Western Interior (*fide* Kennedy *et al.* 1987). *Pseudaspidoceras sorachiense* Matsumoto & Hashimoto (1953: 101, pl. 10 (fig. 1)) also lacks ventrolateral horns and has straighter flank costae at comparable diameters; moreover, no mention is made of the multiplicity of outer ventrolateral tubercles which is a feature of the present species.

Pseudaspidoceras conciliatum (Stoliczka) (1864: 99, pl. 50 (fig. 4), pl. 51 (fig. 1)) is a highly variable species with prominent outer ventrolateral tubercles which, to judge from Stoliczka's (1864, pl. 51 (fig. 1)) illustration, could be the septate bases of ventrolateral horns; if this is so, it is generically distinct from *Ampakabites.* It differs from *M. mocamedensis* in its quadrate whorl section at relatively small size, and its straighter, more prominent ribs.

Pseudaspidoceras footeanum (Stoliczka) (1864: 101, pl. 52 (figs 1–2); Kennedy *et al.* 1987, text-fig. 4) apparently differs from the present species in its straighter flank costae, more compressed whorls at large size, and in lacking the ventrolateral horns of the present material. Howarth (1985: 98, figs 30–33) recently reported this species from the Novo Redondo region of Angola, but at least one of his fragments (the original of his figure 31) has been assigned to *Mammites powelli* Kennedy *et al.* (1987: 42, pl. 3 (figs 1–14), pl. 4 (figs 16–17), text-fig. 2F, G). According to Chancellor (1982) and Bengtson (1983), *Ammonites pedroanus* White (1887: 212, pl. 22 (figs 1–2)) is a subjective junior synonym of *P. footeanum.*

Stratigraphical occurrence

Morrowites mocamedensis (Howarth) is known only from the upper Lower Turonian of Angola.

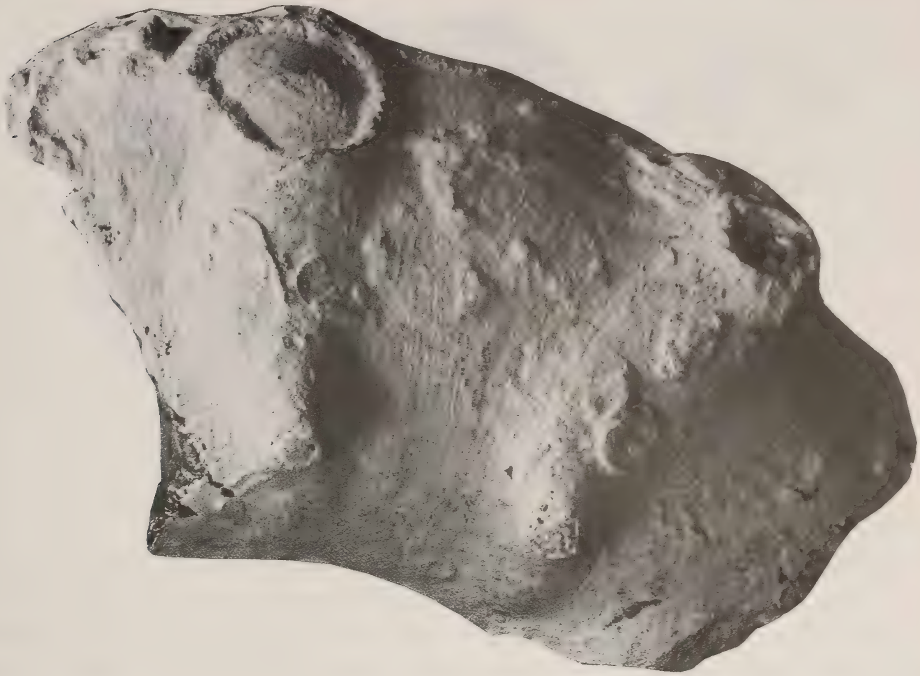

Figure 24

Morrowites mocamedensis (Howarth). × 1. A body-chamber fragment, SAM–PCA1897, showing the septate bases to the ventrolateral horns.

Superfamily COLLIGNONICERATACEAE Wright & Wright, 1951
(*nom. transl.* Cooper 1991 *ex* Collignoniceratidae Wright & Wright, 1951)
Family **Collignoniceratidae** Wright & Wright, 1951
Subfamily Barroisiceratinae Basse, 1947
Genus *Forresteria* Reeside, 1932

Type species

Barroisiceras (Forresteria) forresteri Reeside, 1932; by original designation (Reeside, 1932: 14).

Forresteria sp.
Fig. 25

1976 *Forresteria*? sp.; Cooper, p. 102, pl. 48 (fig. C).

Material

A single eroded specimen, SAM–PCA1846 from Bed V, preserving recrystallized test on one side.

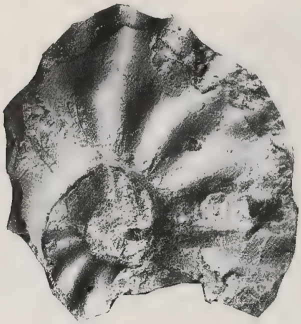

Figure 25

Forresteria sp. × 1.5. Lateral view of SAM–PCA1846.

Description

The shell is poorly preserved due to erosion of one flank and the venter. What remains, however, suggests a fairly evolute, compressed shell with about 30 per cent of the penultimate whorl covered. The umbilicus is rather wide (about 35 per cent of the shell diameter) and fairly deep, with a steep, narrow umbilical wall and gently rounded shoulder. The flanks are broad and convex, with maximum width at midflank, and converge to the narrow, eroded venter. Ornament comprises coarse rectiradiate ribs which arise at the umbilical shoulder and develop into prominent swollen bullae just below midflank. These give rise to two rectiradiate secondaries which are about as wide as the interspaces.

Measurements

Specimen	D	H	W	H/W	U
SAM–PCA1846	*c.* 23	*c.* 14 (*c.* 61)	*c.* 10 (*c.* 43)	*c.* 1.40	*c.* 8 (35)

Discussion

This specimen shows the essential features of the genus but is otherwise too poorly preserved for detailed comparison.

Stratigraphical occurrence

Forresteria is a Lower Coniacian genus, with near cosmopolitan distribution.

Family **Peroniceratidae** Hyatt, 1900
Subfamily Prionocyclinae Breistroffer, 1947
Genus *Prionocyclus* Meek, 1876

Type species

Ammonites novi-mexicani Marcou, 1858 (= *A. serratocarinatus* Meek, 1871*a* (*non*

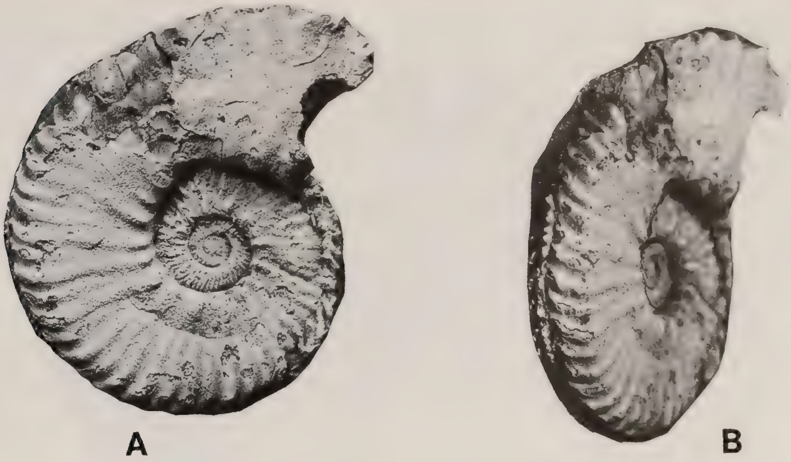

Figure 26

Prionocyclus cf. *novimexicanus* (Marcou). × 1.5. Lateral and oblique lateral views of SAM–PCA1943.

Stoliczka, 1865) = *P. wyomingensis* Meek, 1876); by original designation (Meek, 1871*b*: 298).

Prionocyclus cf. *novimexicanus* (Marcou, 1858)
Fig. 26

Compare

1858	*Ammonites novi-mexicani* Marcou, p. 35, pl. 1 (fig. 2)).
1870	*Ammonites serrato-carinatus* Meek (*non* Stoliczka), p. 429.
1898	*Prionocyclus wyomingensis* (Meek); Logan, p. 463, pl. 106.
1946	*Prionocyclus wyomingensis* (Meek); Haas, p. 200, pl. 18 (figs 3–6), pls 19–24.
1971	*Prionocyclus wyomingensis* (Meek); Matsumoto, p. 132, pl. 21 (fig. 2), pl. 22 (fig. 1), text-fig. 2.
1978*b*	*Subprionocyclus*? sp.; Cooper, p. 4.
1979	*Prionocyclus novimexicanus* (Marcou); Hook & Cobban, p. 34, fig. 3E–L.
1981	*Prionocyclus novimexicanus* (Marcou); Matsumoto *et al.*, p. 4.

Material

A single flattened specimen, SAM–PCA1943, preserving recrystallized test, was picked up in surface scree and is assumed to originate from Bed IV.

Description

The shell is fairly evolute, probably rather compressed, and with about 20 per cent of the preceding whorl covered. The umbilicus is shallow, moderately wide (about 30 per

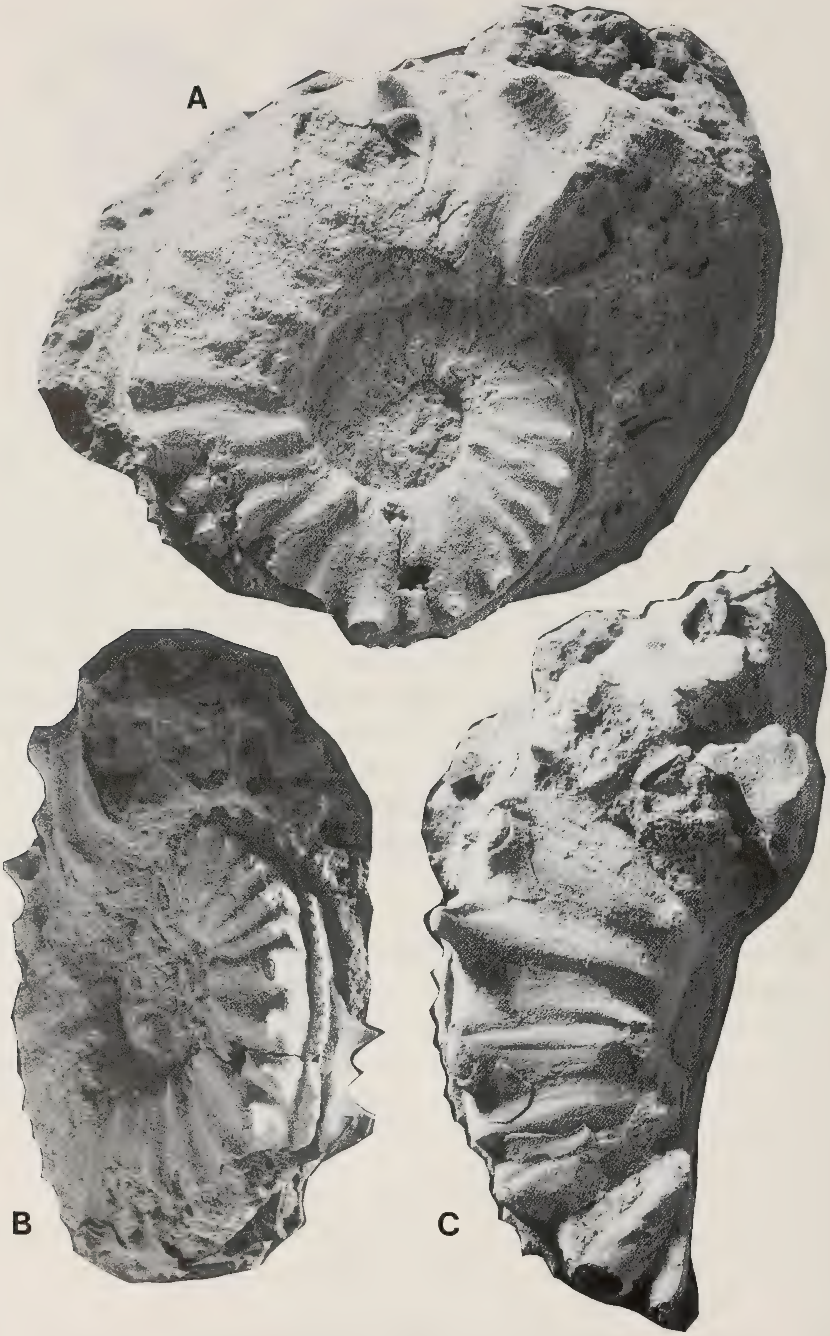

Figure 27

Prionocycloceras carvalhoi (Howarth). × 1. A–B. Lateral and oblique ventral views of SAM–PCA1958. C. Lateral view of SAM–PCA1942.

cent of the shell diameter), and with a steep, narrow umbilical wall and subrounded umbilical shoulder. The flanks are relatively broad and, probably, were almost flat.

Ornament comprises primary ribs that begin at the umbilical seam and pass backwards to the umbilical shoulder where they terminate in about 20 small but distinct umbilical bullae per whorl. These, in turn, give rise singly or in pairs to sinuous, slightly prorsiradiate flank costae which commonly are separated by one, rarely two, intercalated ribs. There are about 50 ribs on the outer whorl, with 14 ribs per 6 umbilical bullae; ribbing weakens slightly on the adoral part of the outer whorl. Each rib is ornamented with paired clavi on the ventrolateral shoulder. Towards the adoral end of the shell, the lower ventrolateral tubercles strengthen and show a tendency to become spinose. From the upper ventrolateral clavi the ribs are weakly projected onto the venter, but they fail to reach the finely serrated siphonal keel. The notches to the siphonal keel greatly outnumber the ventrolateral clavi. There is a distinct oblique constriction near the adapical end of the outer whorl. What can be seen of the penultimate whorl shows dense fine ribbing with frequent bifurcation and intercalation. Suture lines are not displayed. Because the specimen is crushed almost flat morphometric analysis is impossible.

Discussion

Matsumoto (1971) noted the possible synonymy of *P. novimexicanus* and *P. wyomingensis* when describing the latter species from Japan. Subsequently, Matsumoto *et al.* (1981) reassigned the Japanese material to Marcou's (1858) species. Given the wide range of variation documented for this species (Haas 1946), the crushed Angolan specimen is perhaps conspecific, being closest to *P. novimexicanus* var. *elegans* (Haas).

Prionocyclus aberrans Matsumoto (1965: 25, pl. 5 (fig. 1), pl. 6 (fig. 3), text-figs 8–9; 1971: 133, pl. 21 (fig. 1), text-fig. 3) differs from the present species in having coarse, simple flank costae, without bifurcation or intercalation. *Prionocyclus cobbani* Matsumoto (1965: 21, pl. 4 (figs 1–4), text-fig. 7) and *P. reesidei* Sidwell (1932: 318, pl. 49 (figs 10–12); Matsumoto 1965: 21, pl. 17 (fig. 1)) also are more coarsely ribbed, with only 29–38 ribs per whorl, as is *P. hyatti* (Stanton) (1894: 176, pl. 42 (figs 5–8); Matsumoto 1965: 19, pl. 17 (fig. 3)); the latter species also has flank costae differentiated into those that are strong, umbilically bullate and horned, and those that are weak, non-bullate, and hornless (Kennedy & Cobban 1988).

Stratigraphical occurrence

Prionocyclus novimexicanus (Marcou) is known from the upper Middle and low Upper Turonian of North America (Wyoming, S. Dakota, New Mexico), Japan and probably Angola.

Genus *Prionocycloceras* Spath, 1926

Type species

Ammonites guayabanus Steinmann, 1881; by original designation of Spath (1926: 80).

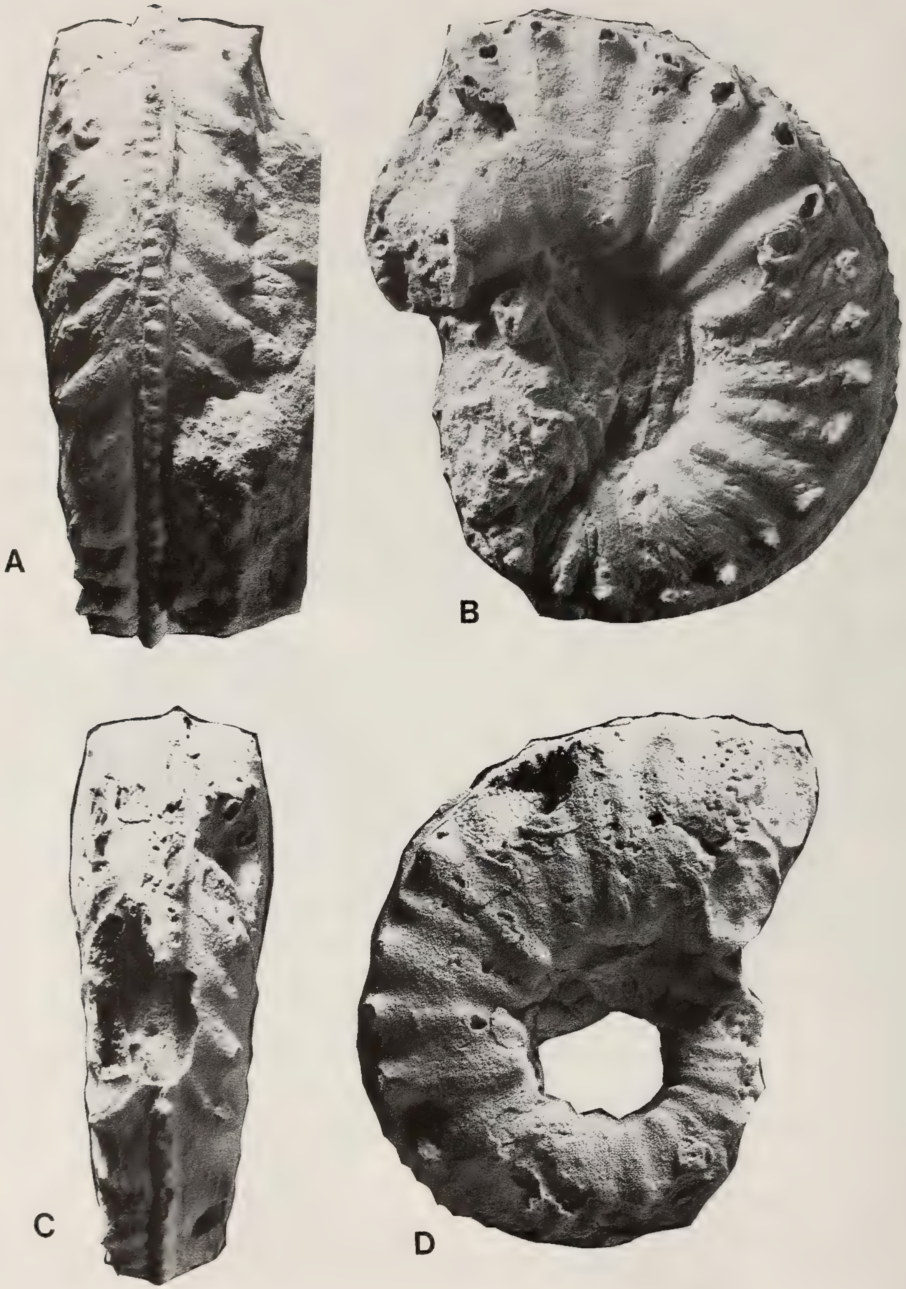

Figure 28

Prionocycloceras carvalhoi (Howarth). × 1. A–B. Ventral and lateral views of SAM–PCA1916. C–D. Ventral and lateral views of SAM–PCA1896.

Prionocycloceras carvalhoi (Howarth, 1968)
Figs 5A–D, 9B–C, 20D, 27–28

?1967	*Prionocycloceras guayabanum* (Steinmann) Collignon, p. 48, pl. 29 (figs 1–3 only).
1968	*Prionocyclus carvalhoi* Howarth, p. 224, pl. 1 (figs 8–11), pl. 2 (figs 3–6).
1978*b*	*Prionocycloceras carvalhoi* (Howarth); Cooper, p. 4, fig. 7.

Material

Many fragmentary specimens, including SAM–PCA1754, 1758, 1832, 1896, 1911, 1916, 1931, 1942, 1944, 1958, and 1965, from Beds V and VI.

Description

The shell is compressed, evolute, with about 15 per cent of the preceding whorl covered. The umbilicus is moderately wide (27–43 per cent of the shell diameter), shallow, with subvertical walls and evenly rounded shoulders. The flat flanks are subparallel and the broad venter is flattened in costal section, resulting in a subquadrate, compressed whorl section (H/W = 1.13–1.42).

Ornament is variable. Ribs begin at the umbilical seam and pass backwards to the umbilical shoulder where they form bullae of variable strength; on SAM–PCA1942 there are conspicuous umbilical spines whereas SAM–PCA1896 and 1911 display irregular tubercle development varying from strengthened growth lines to swollen bullae. From the umbilical tubercles broad, low, indistinct, prorsiradiate ribs cross the flank, separated by narrower interspaces, and terminate in septate ventrolateral spines which are directed diagonally outward on SAM–PCA1758. At diameters of less than 35 mm, weak but distinct ventrolateral clavi are also developed but these become obsolete in maturity. Intercalated ribs are sporadically developed between main ribs and tend to be finer than the latter, with poorly developed ventrolateral spines. Spine prominence is linked to the size of the umbilical bullae; large spines are generally associated with conspicuous bullae and vice versa. Ribs project strongly forwards on the venter, but become effaced before reaching the conspicuously serrated siphonal keel. Serrations far exceed the number of ventrolateral spines, with 11–12 in a distance equal to the whorl height. In maturity the keel thickens and serrations become increasingly indistinct until, finally, only a broad low siphonal hump remains which is crossed by growth striae. Sulci development on either side of the keel is variable in early and middle growth; they are present in SAM–PCA1754, 1758, 1916 and 1942, indistinct in SAM–PCA1911, and lacking from SAM–PCA1931 and 1965. The general tendency is for sulci to shallow and become obsolete at large diameter.

Measurements

Specimen	D	H	W	H/W	U
SAM–PCA1944	?	37	26	1.42	?
SAM–PCA1916	83	33 (40)	*c.* 31 (37)	1.06	28 (34)
SAM–PCA1896	78	34 (44)	25.5 (33)	1.33	28 (36)
"	53	23.5 (44)	20 (38)	1.18	19 (36)
SAM–PCA1958	73	30 (41)	?	?	25 (34)
SAM–PCA1754	?	30	22	1.36	?
SAM–PCA1758	?	43	38	1.13	?
SAM–PCA1807	34	14 (41)	11 (32)	1.27	11,5 (34)
SAM–PCA1942	34	15 (44)	11.5 (34)	1.30	9 (27)
SAM–PCA1832	?	18.5	14.5	1.28	?
SAM–PCA1911	28	13 (46)	10.2 (36)	1.27	12 (43)

Discussion

Howarth (1968: 224) assigned the present species to *Prionocyclus* '… because the keel is bordered by shallow sulci and the ribs are projected strongly forwards on the venter and do not clearly join the keel'. However, the material now available shows much variation in this respect; in addition, the new stratigraphical data show *P. carvalhoi* associated with typical Coniacian forms. This, together with its coarser, sparser, more irregular ribbing and propensity for horn development, suggests better reference to *Prionocycloceras*; there can be no doubt, however, that the latter evolved from the former. The Angolan material is characterized by well-developed but irregular flank ornament, with strong radial ribs bearing spinose umbilical tubercles and long ventrolateral spines.

Moroccan *P. keithyoungi* (Collignon 1967: 49, pl. 30 (figs 3–5)) closely resembles *P. carvalhoi*, but is characterized by migration of the umbilical tubercle up the flank during ontogeny. Collignon (1967) recorded *P. keithyoungi* in association with *P. guayabanum* (Steinmann), but some of his specimens (Collignon 1967, pl. 29 (figs 1–3 only)) differ from true *P. guayabanum* (Steinmann) (Gerhardt 1897: 197, pl. 5 (fig. 22); Young 1963: 67, pl. 23 (figs 5–6), pl. 27 (figs 2–3); Renz 1982: 107, pl. 35 (figs 11–14)) in being more strongly and densely ribbed, with distinct umbilical bullae, and are thus closer to the present species. In view of the high intraspecific variability displayed by the Angolan material, it seems certain that the host of nominal *Prionocycloceras* species are an artefact of polymorphism.

Prionocycloceras portarum Etayo-Serna (1979: 95, pl. 13 (fig. 12), pl. 14 (fig. 4)) displays the subdued, sparse ribbing and very weak umbilical bullae of *P. guayabanum*, and Renz (1982) included it in the synonomy of Steinmann's (*in* Gerhardt 1897) species. According to Young (1963), *Peroniceras (Donjuaniceras) longispinata* Basse (1951: 247, pl. 11 (figs 1–4)) is also a synonym of *P. guayabanum*.

Prionocycloceras mediotuberculatum (Gerhardt) (1897: 198, pl. 5 (fig. 23)) differs from the present species in having uniformly developed, flexuous, main ribs which swell at midflank, with weaker umbilical bullae and no intercalated ribs.

Prionocycloceras wrighti Matsumoto (1971: 134, pl. 22 (fig. 2), fig. 4) is based upon a juvenile that was separated from *P. guayabanum* on differences in the suture line and the presence of doubled ventrolateral tubercles. The Angolan species shows doubled ventrolateral tubercles in the juvenile growth stages and, consequently, the Japanese species is poorly discriminated.

Prionocycloceras adkinsae Young (1963: 69, pl. 23 (figs 1–4), text-figs 25f, 28g, 34e) is based on fragmentary material that is much more coarsely ribbed than the Angolan material. *Prionocycloceras gabrielense* Young (1963: 69, pl. 24 (figs 1–3), pl. 29 (fig. 5), pl. 67 (fig. 1), text-fig. 21c) is difficult to judge but, according to Kennedy & Cobban (1991), is a giant *Protexanites*.

Prionocycloceras crenulatum (Anderson) (1902: 125, pl. 1 (figs 17–18); 1958: 263, pl. 34 (figs 4–5)) differs from the present species in the loss of ventrolateral spines beyond about 50 mm diameter. *Gauthiericeras fauremuretae* Collignon (1967: 50, pl. 28 (fig. 10)) may be a *Prionocycloceras*; it differs from the present material in its denser, more uniform ribbing.

Stratigraphical occurrence

Prionocycloceras carvalhoi (Howarth) is known with certainty only from the Lower Coniacian of Angola, but may be present also in Morocco.

Prionocycloceras sp.

Fig. 9A

Material

A single laterally crushed specimen, SAM–PCA1775, preserving recrystallized test from Bed V.

Description

The shell is evolute, compressed, with about 15 per cent of the preceding whorl covered. The umbilicus is wide and shallow (34 per cent of the diameter), with a fairly steep umbilical wall and evenly rounded umbilical shoulder. The flanks are broad and flat but the nature of the venter and the whorl section are obscured by crushing.

Beyond a diameter of 40 mm, ribbing becomes indistinct and the whorls are essentially smooth save for conspicuous, horizontally directed ventrolateral horns. There are distinct sulci bounding the conspicuously notched siphonal keel.

Measurements

Specimen	D	H	W	H/W	U
SAM–PCA1775	107	42 (39)	?	?	37 (34)

Discussion

Superficially, the present specimen most closely resembles *Prionocycloceras hazzardi* Young (1963: 71, pl. 24 (fig. 4), pl. 25 (figs 2–3), pl. 26 (figs 1–2), pl. 27 (fig. 4), pl. 34 (fig. 2), pl. 39 (fig. 3), text-figs 12f, 13b,d, 14g, 20h; Collignon, 1967: 49, pl. 31 (fig. 1)) but the latter species is a *Protexanites* (*cf.* Matsumoto 1965) and the Angolan specimen retains the finely serrated keel of *Prionocycloceras*. It differs from *P. carvalhoi* (Howarth) in that its ribbing becomes indistinct beyond 40 mm diameter, umbilical bullae are lacking, and the ventrolateral spines are directed horizontally outwards. Perhaps it is merely an aberration.

Stratigraphical occurrence

Prionocycloceras sp. is currently known only from the Lower Coniacian of Angola.

AGE RELATIONSHIPS OF THE FAUNA

Bed I of the São Nicolau succession did not contain ammonites but Bed II yielded *Vascoceras* cf. *proprium* (Reyment) and *Morrowites mocamedensis* (Howarth). Since *Morrowites* is believed to have evolved from uppermost Cenomanian-basal Turonian *Pseudaspidoceras*, Bed 2 belongs to a level above the base of the Turonian. Bed III did not yield ammonites.

Bed IV yielded *Anagaudryceras involvulum* (Stoliczka), *Hypophylloceras* sp. nov.?, *Placenticeras kaffrarium* Etheridge (*kaffrarium* morphotypes only), *Tetragonites glabrus* Jimbo, *Mossamedites serratocarinatus* (Kennedy & Cobban), and *Puebloites greenhornensis* Cobban & Scott. Although most of these taxa are long ranging and do not provide precise age determinations, *M. serratocarinatus* (Kennedy & Cobban) occurs in the upper part of the Middle Turonian in New Mexico and serves to date Bed IV. This is probably also the level of *Prionocyclus* cf. *novimexicanum* (Marcou). The bivalve *Acanthotrigonia shepstonei* (Griesbach) also occurs in this bed, and this occurrence represents the earliest record of the genus.

Bed V dates to the lowest Coniacian on the basis of the occurrence of *Prionocycloceras carvalhoi* (Howarth) and *Forresteria* sp.; less-diagnostic species from this level include *Placenticeras kaffrarium* Etheridge, *Damesites ainuanus* Matsumoto, *Tetragonites glabrus* Jimbo, *Gaudryceras mite* (von Hauer), *Anagaudryceras involvulum* (Stoliczka), *Baculites klingeri* sp. nov., *Tongoboryceras*? sp., and *Hypophylloceras* sp. juv.

Bed VI is still Lower Coniacian, with abundant *Prionocycloceras carvalhoi* (Howarth) and *Veniella forbesiana* (Stoliczka), together with *Kossmaticeras theobaldianum* (Stoliczka) and *Placenticeras kaffrarium* Etheridge.

Beds VII and VIII contained no ammonites and Bed IX, the highest exposed bed in the gullies, yielded only *Mesopuzosia indopacifica* (Stoliczka), a Middle Turonian to Lower Coniacian species.

Almost the entire Turonian succession at São Nicolau therefore is condensed into only 3 m of thin fossiliferous limestones and unfossiliferous siltstones, with the latter predominant. By contrast, the overlying 7 m of the exposed section suggest only the Petrocoriensis Zone at the base of the Coniacian is represented.

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STRATIGRAPHY AND PALAEONTOLOGY OF THE UPPER CRETACEOUS (SANTONIAN) BABA FORMATION AT SÃO NICOLAU, ANGOLA

by

MICHAEL ROBERT COOPER

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STRATIGRAPHY AND PALAEONTOLOGY OF THE UPPER CRETACEOUS (SANTONIAN) BABA FORMATION AT SÃO NICOLAU, ANGOLA

by

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With 9 figures

[*MS submitted March 1998*]
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ABSTRACT

The stratigraphy and palaeontology of the Baba Formation is described from west of São Nicolau in the Moçâmedes Desert. The transgressive-regressive succession is divided into a lower unit of richly fossiliferous marine limestones and fine-grained clastics, the Caniço Member (new term), and an upper unit of nearshore coarse clastics, the Bero Member. Ammonites from the Caniço Member include *Texanites*, ?*Protexanites*, *Hauericeras (Gardeniceras)* and *Damesites*, and serve to date both the base of the Baba Formation and a major transgressive event to the Middle Santonian. This indicates a Middle Coniacian to Lower Santonian age for basaltic lavas of the Ombe Formation.

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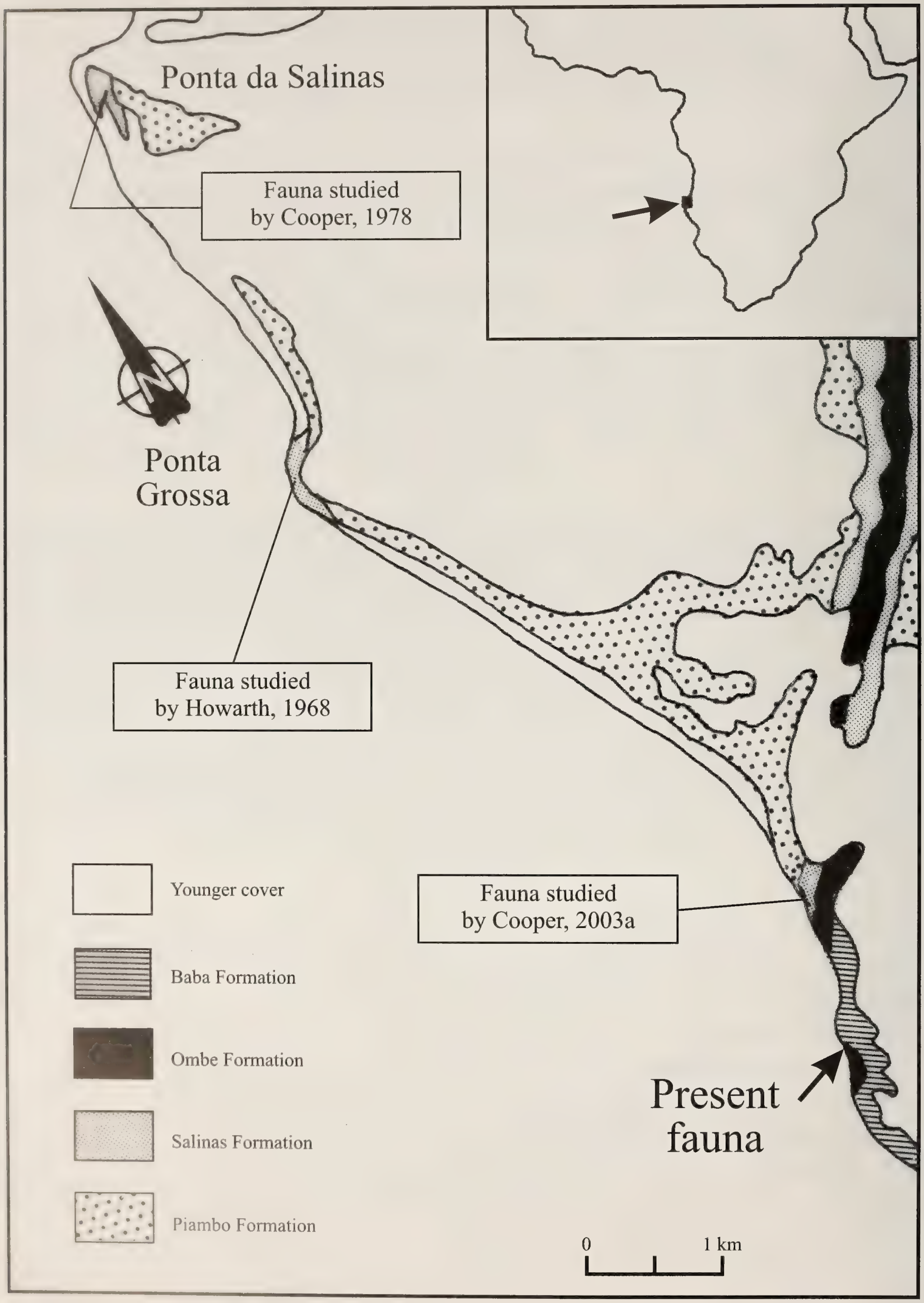

Figure 1

Locality map showing distribution of the São Nicolau Group in the vicinity of the Farol de Ponta Grossa. Adapted from Carvalho (1961).

INTRODUCTION

This paper continues the writer's account of the Cretaceous ammonite faunas and stratigraphy of Angola (Cooper 1972, 1973, 1974, 1983, 1989; Cooper & Kennedy 1979), and concerns the Baba Formation at São Nicolau (Fig. 1).

Mouta & Borges (1926) were the first to study this lithostratigraphical unit; based on occurrence of the bivalves *Crassatella numidica* Munier-Chalmas, *Cardita beaumonti* d'Archiac and *Roundaireia drui* Munier-Chalmas, they assigned a Senonian age to the Baba Formation. This age was confirmed by Rennie's (1929) study of Mollusca from the stratotype at Baba (some 60 km to the south of the present locality); identification of *Trigonarca angolensis* Rennie, *T.* cf. *trichinopolitensis* (Forbes), *Nemodon natalensis* (Baily), *Veniella drui* (Munier-Chalmas), *Cardita barroneti* Munier-Chalmas, *Cardium (Trachycardium) reynoldsi* Rennie, *Tellina (Palaeomoera?)* sp. and *Turritella (Haustator?)* cf. *acanthophora* (Müller) led Rennie (1929) to assign a Campanian–Maastrichtian age to the deposit. This determination was repeated by Mouta & O'Donnell (1933) and Mouta (1938).

Subsequent work has centred around the present exposures at São Nicolau; from here Rennie (1945) identified *Trigonia (Scabrotrigonia) shepstoni* Griesbach, *Turritella (Zaria) bonei* Baily, and *Lima (Mantellum)* sp., revising the age of the Baba Formation to Campanian. Borges (1946; cited in Carvalho 1961) listed nine molluscan species from immediately above the basalts at São Nicolau, but these identifications are suspect. Most recently, Spath (1951) identified *Eutrephoceras indicum* (Spengler) (= *E. spengleri* Wiedmann) and *Baculites* aff. *asper* (Morton) from collections made by O'Donnell at São Nicolau.

The lithostratigraphy of the Baba Formation in the Moçâmedes Desert was described in detail by Carvalho (1961) and this worker accepted the Campanian age ascribed these rocks. However, Cooper (1972, 1979) described the Cretaceous stratigraphy of the region around São Nicolau and Salinas and, on the basis of preliminary ammonite identifications, assigned an early Santonian age to the sediments overlying the volcanics, i.e. the Caniço Member.

STRATIGRAPHY

Cooper (1979) first applied formal lithostratigraphical nomenclature to the Cretaceous succession of the Moçâmedes desert. The Baba Formation was introduced for marine sediments which disconformably overlie the Ombe Volcanic Formation and are, in turn, overlain disconformably by the Mocuio Formation with a basal bone bed rich in vertebrate remains. The latter, which include *Mososaurus beaugei* Arambourg and selachian teeth assigned to *Squalicorax pristodontus* (Agassiz), *S. kaupi* (Agassiz), *Cretolamna biauriculata moroccana* (Arambourg), *Carcharias subulata* (Agassiz), *Rhombodus binkhorsti* Dames, *Enchodus elegans* Darteville & Casier, *E. lybicus* Quaas, *E. bursauxi* Arambourg and *E. lemonnieri* Dollo (Darteville & Casier 1941, 1946; Darteville 1942; Carvalho 1961), serve to date the Mocuio Formation to the uppermost Campanian/Maastrichtian.

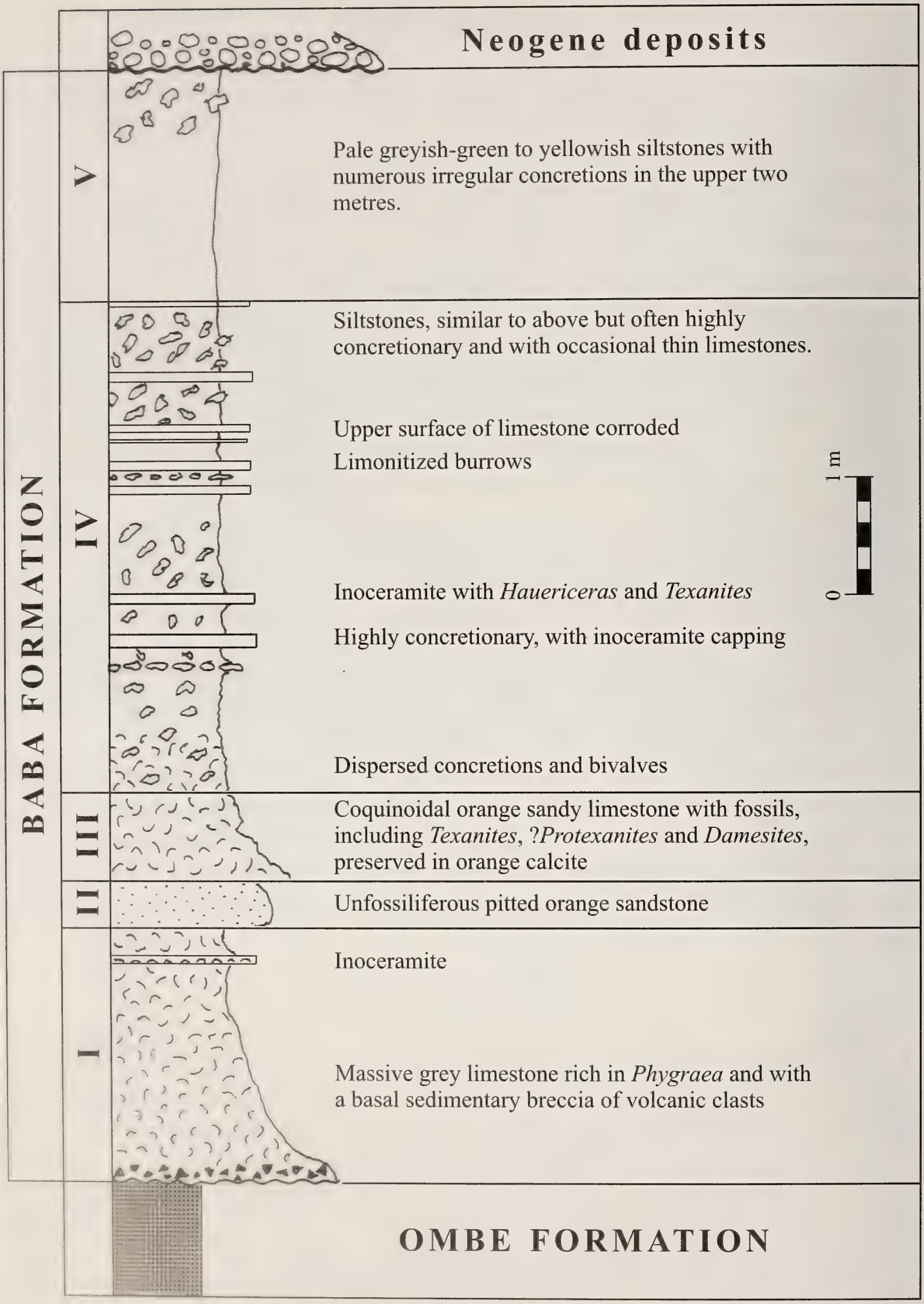
Neogene deposits
BABA FORMATION
V
Pale greyish-green to yellowish siltstones with numerous irregular concretions in the upper two metres.
IV
Siltstones, similar to above but often highly concretionary and with occasional thin limestones.
Upper surface of limestone corroded
Limonitized burrows
1 m
0
Inoceramite with *Hauericeras* and *Texanites*
Highly concretionary, with inoceramite capping
Dispersed concretions and bivalves
III
Coquinoidal orange sandy limestone with fossils, including *Texanites*, ?*Protexanites* and *Damesites*, preserved in orange calcite
II
Unfossiliferous pitted orange sandstone
I
Inoceramite
Massive grey limestone rich in *Phygraea* and with a basal sedimentary breccia of volcanic clasts
OMBE FORMATION

Figure 2

Measured section through the Caniço Member, Baba Formation, west of São Nicolau.

Carvalho (1961) identified a fundamental division within the Baba Formation, separating a lower unit of richly fossiliferous marine limestones and fine-grained clastics from the conformably overlying coarse clastics (with inoceramid prisms) of the Bero Conglomerate Member. This division is widespread in the Moçâmedes Desert and it is proposed here to recognize these lithological differences formally, with the introduction of the Caniço Member. The stratotype for the latter unit is in the Damba do Caniço, to the south of Chapéu Armado (cf. Carvalho 1961).

To the south-east of the Farol de Ponta Grossa (Fig. 1), the Baba Formation is represented only by the Caniço Member, which here comprises a succession of fossiliferous limestones and decalcified fine-grained clastics with concretionary horizons and layers of inoceramite (Fig. 2). These marine sediments rest disconformably on the Ombe Formation with a basal sedimentary breccia of volcanic clasts and, in turn, are disconformably overlain by Neogene conglomerates ('Tirreniano' *fide* Carvalho (1961), but probably Pliocene). Fossils, which are most abundant in the lower part of the Caniço Member, are dominated by bivalves (Figs 3–5). The collections in the South African Museum include *Neithea (Neithea) quinquecostata* (J. Sowerby), *Acanthotrigonia* sp. juv., *Veniella undata* (Conrad), *Protocardia* cf. *umkwelanensis* (Etheridge), *Trachycardium* cf. *reynoldsi* (Rennie), *Oscillopha* cf. *dichotoma* (Bayle), *Plicatula* aff. *auressensis* (Coquand) and *Phygraea* aff. *newberryi* (Stanton), with which are associated the echinoid *Bolbaster* and occasional, mostly unidentified gastropods. The ammonites described here come from units II and III of the stratigraphic column.

Because Santonian macrofossil biostratigraphy is poorly known in detail, the precise age of the succession is problematical. The association of *Texanites* + *Hauericeras (Gardeniceras)* immediately brackets the Caniço Member into the Santonian–Lower Campanian. Although the presence of ?*Protexanites* in unit II led Cooper (1972) to favour an early Santonian age for the Caniço Member, this ammonite genus is now known to extend into the Upper Santonian (Toshimitsu 1988).

The relative abundance of *Hauericeras (Gardeniceras) gardeni* (Baily) and *Texanites venustus* Collignon in the São Nicolau fauna is believed to be biostratigraphically meaningful since these taxa first appear only in the Middle Santonian 'Zone à *Texanites hourcqui*' of Madagascar (Besairie 1972: 285) and, likewise, are absent from the Lower Santonian of Zululand (pers. obs.). The balance of faunal evidence favours, therefore, a mid-Santonian age for the Caniço Member at São Nicolau. This determination, together with the early Coniacian age assigned to the uppermost observed levels of the Salinas Formation, serves to date Ombe volcanism as Middle Coniacian to Lower Santonian.

A mid-Santonian age for the marine transgression responsible for Baba sedimentation is of some significance, since it is of identical age to the major late Cretaceous transgressive event along the east coast of Africa (Cooper 1974, 1976), and accounts for the similarity between the Baba and Mzamba molluscan faunas (Rennie 1945; Carvalho 1961). The overlying Bero Conglomerate, a proximal shoreline facies, indicates shoaling upward and deposition of the upper Baba Formation under regressive conditions; unfortunately, the latter phase is not yet dated precisely. However, the transgressive-regressive cycle responsible for deposition of the Baba Formation is believed to correlate

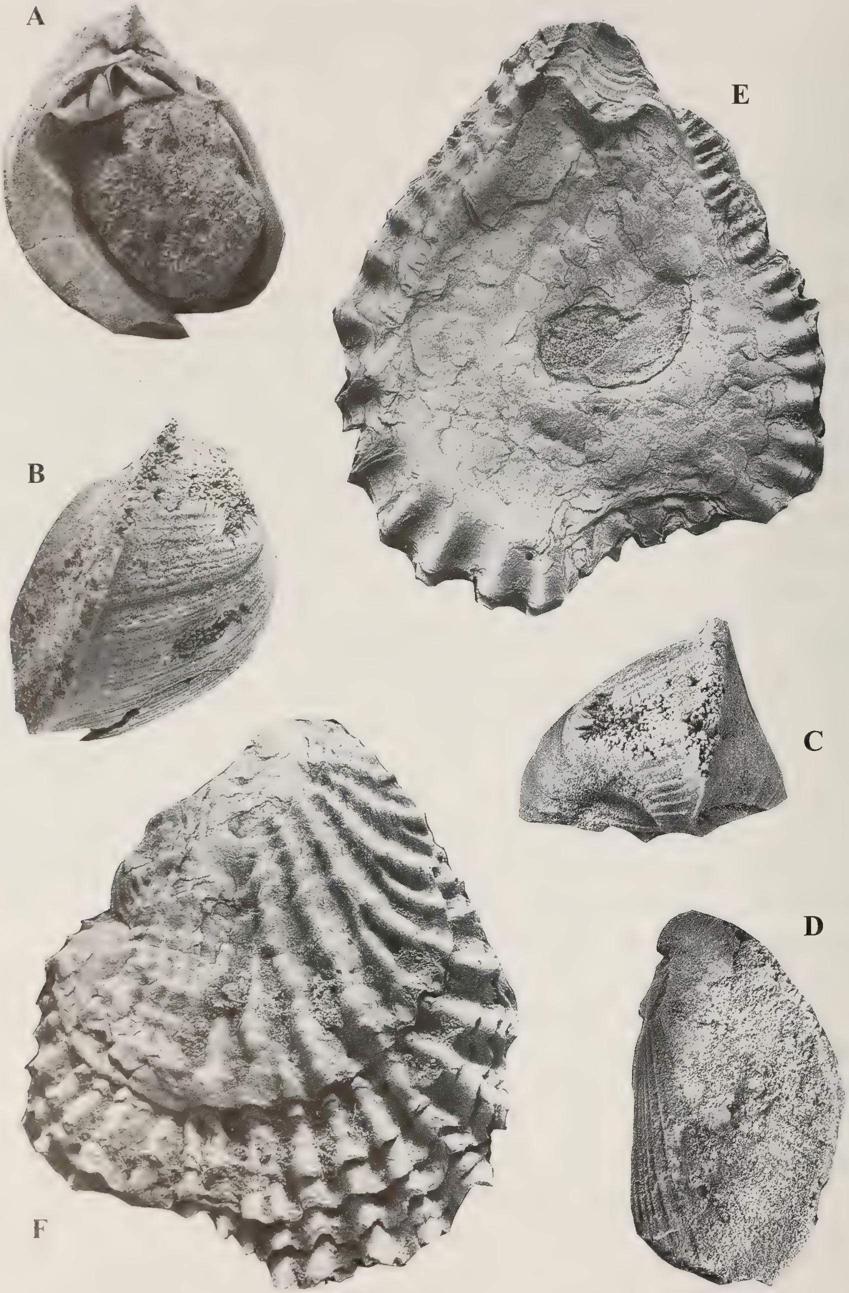

Figure 3

A–D. *Veniella undata* (Conrad). × 1. Interior, lateral, dorsal and anterior views of a left valve, SAM–PCA1976. E–F. *Oscillopha* cf. *dichotoma* (Bayle). × 1. Internal and external views of a right valve, SAM–PCA1989.

with Sequence 32 of the global sea-level curve (Haq et al. 1987).

All the material described here is housed in the South African Museum, Cape Town. Abbreviations for measurements are as follows: D = shell diameter, H = whorl height, W = whorl width, U = umbilical diameter, *c.* = circa, applies to measurements which have been estimated, whether due to erosion, damage or distortion; all measurements are followed, in parentheses, by the dimension as a ratio of the shell diameter.

SYSTEMATIC PALAEONTOLOGY

Subclass AMMONOIDEA Zittel, 1884
Order AMMONITIDA Agassiz, 1847
Suborder TURRILITINA Besnosov & Mikhailova, 1983
Superfamily BACULITACEAE Gill, 1871
Family **Baculitidae** Gill, 1871
Genus *Baculites* Lamarck, 1799

Type species

Baculites vertebralis Lamarck, 1799; by the subsequent designation of Meek, 1876.

Baculites aff. *bailyi* (Woods, 1906)

Compare

1906	*Baculites bailyi* Woods, p. 341, pl. 44 (fig. 5).
1951	*Baculites* aff. *asper* (Morton); Spath, 1951: 127.

Material

Three very small fragments, SAM–PCA2042, 2045–6, preserved as internal moulds.

Description

Typically baculitid, with a straight tapering shaft and compressed, elliptical whorl section. Except for some very faint undulations across the venter, ornament appears to be lacking but this may be due to erosion.

Discussion

The above material is too poorly preserved for proper identification and does not warrant figuring. However, its lack of ornament and age suggests comparison with Wood's (1906) species. As the material recorded by Spath (1951) as *Baculites* aff. *asper* (Morton) comes from the same locality it is probably conspecific.

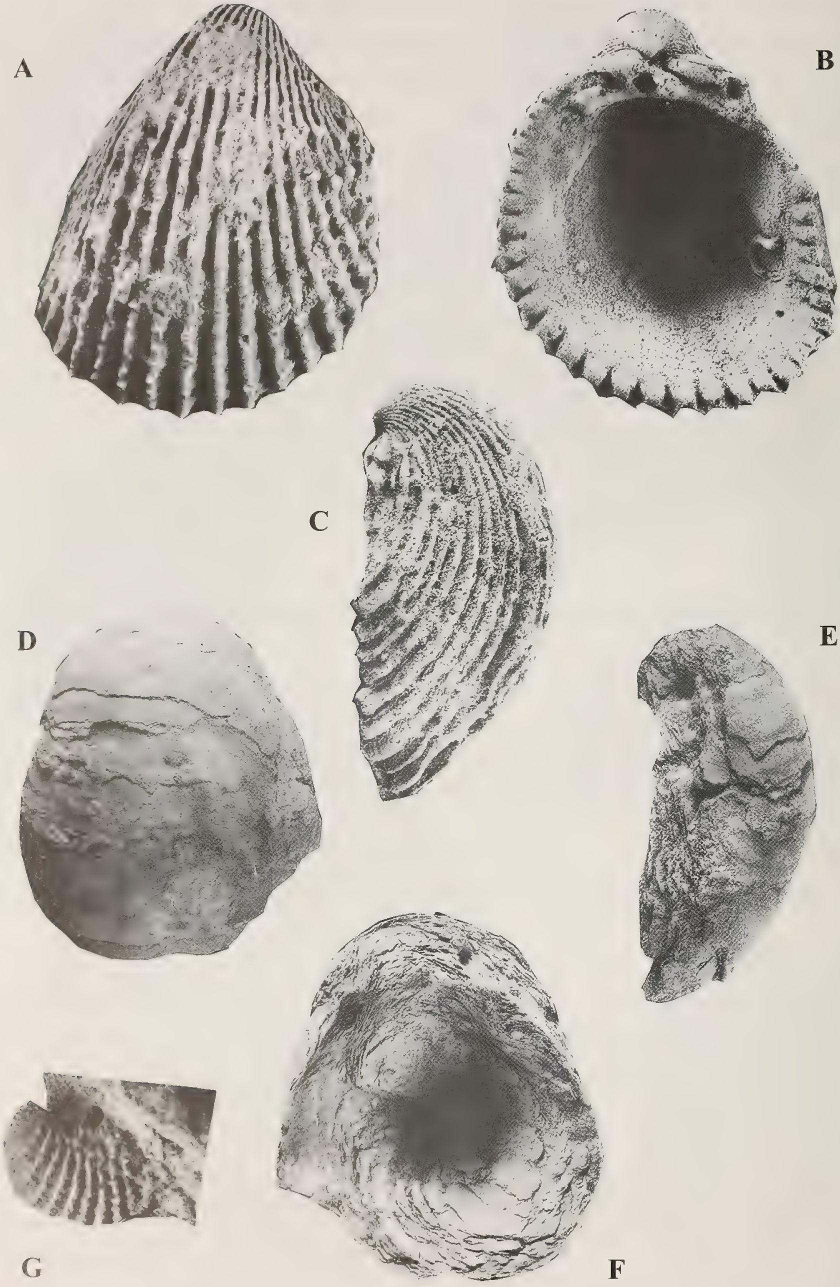

Figure 4

A–C. *Trachycardium* cf. *reynoldsi* (Rennie). × 2. Lateral, interior and anterior views of a right valve, SAM–PCA1984. D–F. *Phygraea* aff. *newberryi* (Stanton). × 1. Lateral, anterior and internal views of a left valve., SAM–PCA8531. G. *Acanthotrigonia* sp. juv. × 2. Lateral view of a left valve, SAM–PCA3613.

Suborder HOPLITINA Spath, 1925
Superfamily DESMOCERATACEAE Zittel, 1895
Family **Desmoceratidae** Zittel, 1895
Genus *Damesites* Matsumoto, 1942

Type species

Desmoceras damesi Jimbo, 1894; by original designation.

Damesites sugata (Forbes, 1846)
Figs 6E–F, 7D

1846	*Ammonites sugata* Forbes, p. 113, pl. 10 (fig. 2).
1898	*Desmoceras sugata* (Forbes); Kossmat, p. 176, pl. 18 (fig. 11), pl. 19 (fig. 1).
1902	*Desmoceras sugatum* (Forbes); Anderson, p. 98, pl. 3 (figs 98–99).
1954	*Damesites sugata* (Forbes); Matsumoto, p. 266.
1955	*Damesites sugata* (Forbes); Matsumoto & Obata, p. 128, pl. 26 (figs 4–5), pl. 27 (figs 3–4).
1957	*Damesites sugata* (Forbes); Matsumoto, p. 87.
1958	*Kotôceras subsugatum* Anderson, p. 217, pl. 35 (fig. 2).
1958	*Kotôceras richardsoni* Anderson, p. 217, pl. 36 (fig. 3).
1958	*Kotôceras frazierense* Anderson, p. 217, pl. 40 (fig. 5).
1959	*Damesites sugata* (Forbes); Matsumoto, p. 12.
1961	*Damesites sugata* (Forbes); Collignon, p. 71 (figs 1–2).
1970	*Damesites damesi* var. *intermedia* Jeletzky (*non* Matsumoto), *in* Muller & Jeletzky, p. 38.
1988	*Damesites sugata* (Forbes); Toshimitsu, p. 191.
1989	*Damesites sugata* (Forbes); Haggart, p. 195, pl. 8.4 (figs 14–23).

Material

A single specimen, SAM–PCA1968, preserving recrystallized test.

Description

The shell is compressed, extremely involute, with the outer whorl covering virtually the entire penultimate whorl. The umbilicus is very narrow (8% of the diameter) and deep, with a strongly convex umbilical wall that overhangs the seam and an evenly rounded shoulder. The broad flanks are weakly convex, with maximum width slightly above midflank, and the venter is rounded with a well-developed but narrow siphonal keel. The whorl section (Fig. 4D) is somewhat compressed, higher than wide (H/W = 1.21). The flanks are smooth with no sign of ornament and constrictions are lacking.

Measurements

Specimen	D	H	W	H/W	U
SAM–PCA1968	36.2	22.3 (0.60)	16.8 (0.45)	1.33	3 (0.08)

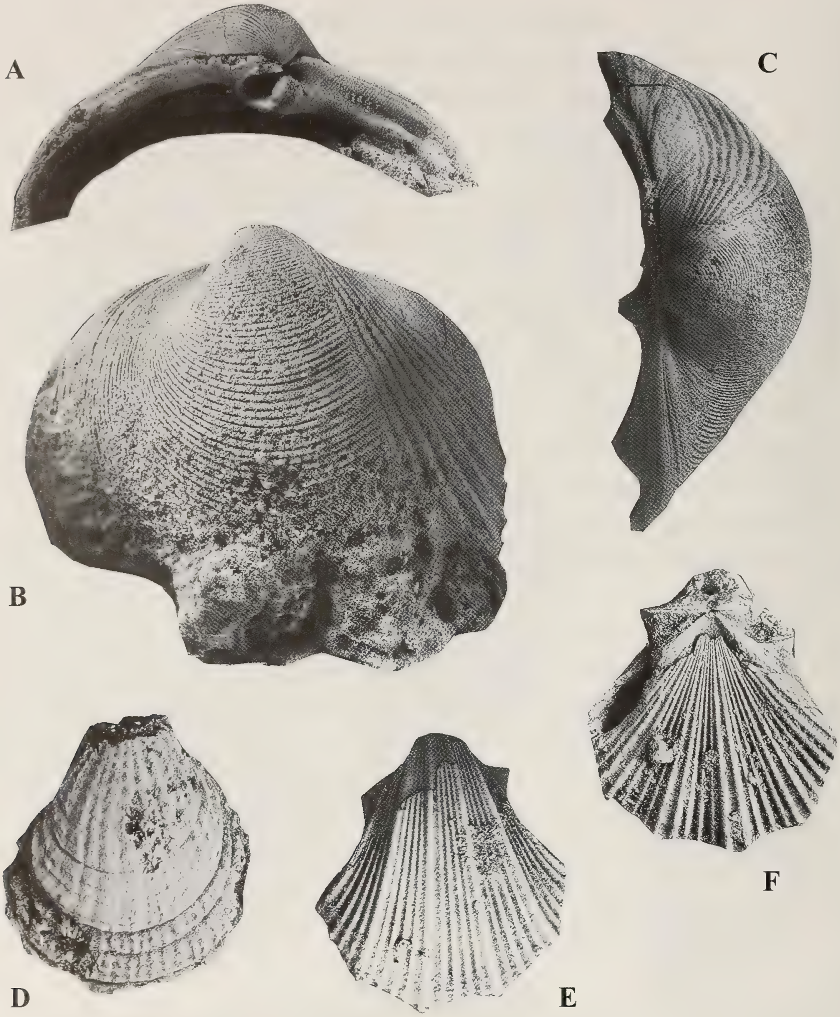

Figure 5

A–C. *Protocardia* cf. *umkwelanensis* (Etheridge). × 1. Hinge, lateral and dorsal views of a left valve, SAM–PCA3613. D. *Plicatula* aff. *auressensis* (Coquand). ×1.5. Lateral view of SAM–PCA1700. E–F. *Neithea* (*Neithea*) *quinquecostata* (J. Sowerby). × 1.5. Lateral views of the left and right valves of SAM–PCA1705.

Discussion

The present material agrees well with Forbes' (1846) illustration and is considered conspecific. It differs from contemporaneous *D. compactus* (van Hoepen) (1921: 21, pl. 4 (figs 5–7)) and Lower Campanian *Damesites rabei* Collignon (1961: 72, pl. 27 (fig. 3)) in having maximum width just above midflank and not at the ventrolateral shoulders.

Damesites damesi (Jimbo) (Matsumoto 1954: 267, pl. 5 (figs 1–3), text-figs 10–11) is a long-ranging, poorly characterized contemporary of *D. sugata*, which seems to differ only in having flexuous constrictions. Significantly, *D. damesi intermedius* Matsumoto (1954: 270, pl. 6 (fig. 4); Matsumoto & Obata 1955: 131, pl. 27 (figs 1–2)) is claimed to be transitional between the two and Haggart (1980) suggested that this subspecies is better included in the synonymy of *D. sugata*.

Lower Santonian *Damesites tsianalokyensis* Collignon (1961: 73, pl. 27 (figs 4–6), text-fig. 11) is a Madagascan species that differs from the Angolan specimen in being more involute, with more inflated whorls and very fine flexuous lirae.

Damesites ainuanus Matsumoto (1957: 86, pl. 15 (figs 1–2)) is a Turonian–Coniacian species distinguished from *D. sugata* by its broader, lower siphonal keel. *Damesites laticarinatus* Saito & Matsumoto (1956: 192, fig. 1) from the Cenomanian of Japan has an even lower keel than *D. ainuanus*.

Damesites hetonaiensis Matsumoto (1954: 271, pl. 6 (figs 1–3), text-fig. 12) is an Upper Campanian to Maastrichtian species which was said to differ from *D. sugata* in having weaker constrictions, a narrower umbilicus, and somewhat more inflated whorls. *Damesites hetonaiensis fresnoensis* (Anderson) (1958: 218, pl. 57 (figs 1–5); Matsumoto 1959: 14) is larger than the nominate subspecies and with conspicuous flexuous lirae.

Damesites semicostatus Matsumoto (Matsumoto & Obata 1955: 133, pl. 26 (fig. 2), pl. 30 (fig. 6)) differs from *D. sugata* in possessing pronounced, weakly flexuous lirae.

Occurrence

Damesites sugata (Forbes) ranges from Coniacian to Campanian and is known from southern India (Forbes 1846; Kossmat 1895), Madagascar (Collignon 1961, 1966), Zululand (pers. obs.), California (Matsumoto 1959), British Columbia (Haggart 1989), Japan (Matsumoto & Obata 1955; Toshimitsu 1988), and now Angola.

Family **Pachydiscidae** Spath, 1922

Genus *Menuites* Spath, 1922

Type species

Ammonites menu Forbes, 1846; by original designation.

Menuites sp.

Fig. 8H–K

Material

Two specimens, the one a moderately large, highly eroded internal mould, SAM–PCA1706, and the other a juvenile preserving recrystallized test, SAM–PCA2016.

Description

The shell of SAM–PCA1706 appears to have been moderately inflated and fairly involute, with *c.* 70 per cent of the preceding whorl covered. The umbilicus is moderately wide and fairly deep, with gently sloping umbilical wall and evenly rounded umbilical shoulder. The flanks are strongly convex and converge to the evenly arched venter. The

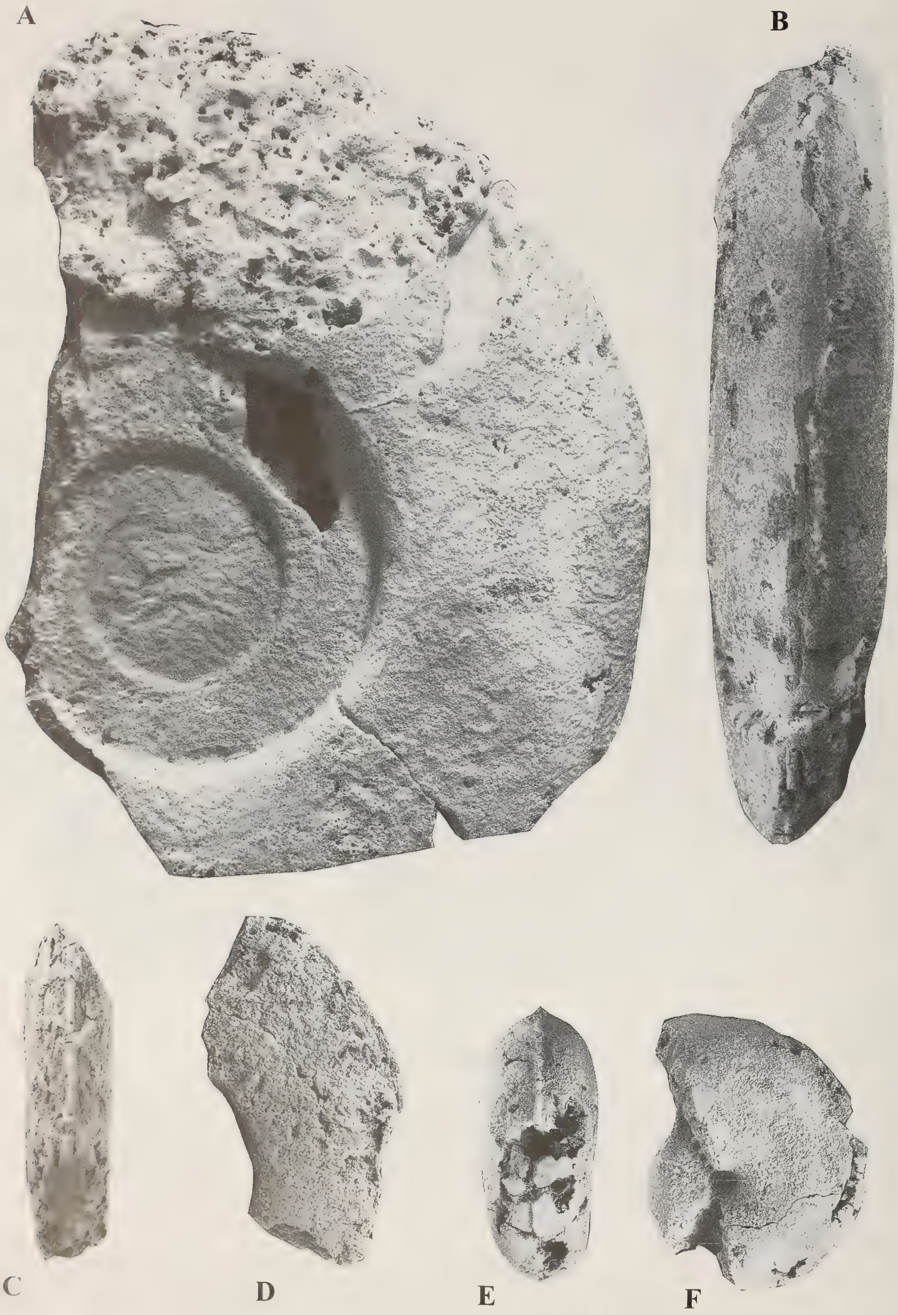

Figure 6

A–D. *Hauericeras* (*Gardeniceras*) *gardeni* (Baily). × 1. A–B. Lateral and ventral views of SAM–PCA1692. C–D. Ventral and lateral views of SAM–PCA1693. E–F. *Damesites sugata* (Forbes). × 1. Ventral and lateral views of SAM–PCA1968.

only ornament is periodic prorsiradiate ribs (?constrictions), but the specimen gives the impression of having had these separated by weakly developed ribs.

The better-preserved juvenile shell, SAM–PCA2016, is compressed, moderately involute, with *c.* 60 per cent of the penultimate whorl covered. The fairly narrow umbilicus (27–31% of the diameter) is rather deep, with a steep umbilical wall and evenly rounded shoulder, and the convex flanks converge towards the narrowly arched venter. Ornament comprises prominent periodic constrictions that flex forwards slightly near the venter and, on the adoral half of the outer whorl, are separated by very weak, indistinct, flexuous riblets.

Measurements

Specimen	D	H	W	U
SAM–PCA2016	22	10 (0.45)	?	6 (0.27)
"	16	8 (0.50)	7.5 (0.47)	5 (0.31)

Discussion

The weak ornament of the Angolan material suggests it is a species of *Menuites*. However, the available material is either too poorly preserved or too immature for positive identification, and comparison with other species is unwarranted.

Occurrence

Menuites is a Campanian genus (Wright 1996).

Family **Puzosidae** Spath, 1922
Subfamily Hauericeratinae Matsumoto, 1938
Genus *Hauericeras* de Grossouvre, 1894
Subgenus *Gardeniceras* Matsumoto & Obata, 1955

Type species

Ammonites gardeni Baily, 1855; by original designation.

Discussion

For the most recent concepts of this genus the reader is referred to Matsumoto *et al.* (1990).

Hauericeras (*Gardeniceras*) *gardeni* (Baily, 1855)
Fig. 6A–D

1855	*Ammonites gardeni* Baily, p. 450, pl. 9 (fig. 3).
1865	*Ammonites gardeni* Baily; Stoliczka, p. 61, pl. 33 (fig. 4).
1890	*Desmoceras gardeni* (Baily); Yokoyama, p. 184, pl. 20 (fig. 10).

1894 *Hauericeras gardeni* (Baily); De Grossouvre, p. 219.
1898 *Hauericeras gardeni* (Baily); Kossmat, p. 123, pl. 18 (figs 7–8, 10).
1907 *Hauericeras gardeni* (Baily); Pervinquière, p. 166, pl. 7 (figs 1, 3–6).
1921 *Hauericeras gardeni* (Baily); Van Hoepen, p. 27, fig. 15.
1921 *Hauericeras gardeni* (Baily); Spath, p. 238, fig. A, 1–9.
1931 *Hauericeras gardeni* (Baily); Basse, p. 23, pl. 4 (figs 2–4), pl. 10 (fig. 8), pl. 11 (fig. 1).
1932 *Hauericeras gardeni* (Baily); Collignon, p. 17, pl. 3 (fig. 3).
1952 *Hauericeras gardeni* (Baily); Usher, p. 65, pl. 5 (figs 1–2), pl. 21 (fig. 10).
1955 *Hauericeras* (*Gardeniceras*) *gardeni* (Baily); Matsumoto & Obata, p. 140, figs 8–12.
1961 *Hauericeras* (*Gardeniceras*) *gardeni* (Baily); Collignon, p. 76, pls 28–29, 30 (figs 1–2)
1969 *Hauericeras* (*Gardeniceras*) *gardeni* (Baily); Collignon, p. 66, pl. 539 (fig. 2114).
1979 *Hauericeras* (*Gardeniceras*) *gardeni* (Baily); Summesberger, p. 133, pl. 6 (fig. 27); text-fig. 19.
1982 *Hauericeras gardeni* (Baily); Immel *et al.*, pl. 16, pl. 5 (fig. 1), pl. 6 (fig. 1), figs 2–4.
non 1982 *Hauericeras* (*Gardeniceras*) aff. *gardeni* (Baily); Renz, p. 106, pl. 35 (figs 2–4) (= *Hauericeras* (*Hauericeras*) sp.).
1987 *Hauericeras gardeni* (Baily); Immel, p. 91.
1990 *Hauericeras* (*Gardeniceras*) *gardeni* (Baily); Matsumoto et al., p. 451.

Material

Nineteen highly eroded, very fragmentary, poorly preserved specimens including SAM–PCA1692 and 1693.

Description

The shell is strongly compressed, very evolute, with a wide shallow umbilicus. The umbilical wall is steep, convex, with a subrounded shoulder, and the broad, weakly convex flanks converge to the narrowly arched, keeled venter. The whorls are strongly compressed, higher than wide (H/W = 1.61–1.96), with a lanceolate section. Ornament and constrictions are not preserved and the material is too poorly preserved for reliable morphometric analysis.

Discussion

Differences between *Hauericeras (Gardeniceras)* species have been covered by Matsumoto & Obata (1955) and Matsumoto *et al.* (1990), and need not be repeated here.

Occurrence

Hauericeras (Gardeniceras) gardeni (Baily) is typical of Middle Santonian to Lower Campanian strata and is reported from Austria (Summesberger 1979), Madagascar (Collignon 1961, 1966), Zululand (Kennedy & Klinger 1975), Transkei (Baily 1855; Van Hoepen 1921), Japan (Matsumoto & Obata 1955), British Columbia (Usher 1952), and now Angola.

Suborder ACANTHOCERATINA Hyatt, 1900
Superfamily COLLIGNONICERATACEAE Wright & Wright, 1951
Family **Texanitidae** Collignon, 1948
Subfamily Texanitinae Collignon, 1948
Genus *Protexanites* Matsumoto, 1955

Type species

Ammonites bourgeoisi d'Orbigny, 1842; by original designation.

?*Protexanites* sp. indet.

Material

A single whorl fragment, SAM–PCA2015, preserving recrystallized test.

Description

The shell was undoubtedly evolute, with a wide shallow umbilicus. The whorl section (Fig. 7C) is compressed (H/W = 1.27), elliptical in intercostal section but polygonal costally, with maximum width about a third of the way up the flank. The rectiradiate ribs begin at sharp umbilical tubercles, swell at midflank without developing a tubercle, and join prominent, swollen, clavate marginal tubercles from which they project forwards to terminate in extremely elongate external clavi. The latter are separated from the siphonal keel by narrow sulci.

Discussion

The strong ornament and trituberculate ribs of the available fragment suggest reference to *Protexanites*. Normally, the inner whorls of *Plesiotexanites* which, also, are trituberculate, do not have the very strongly clavate external tubercles of the Angolan specimen (H. C. Klinger, pers. comm. 1990).

Occurrence

Protexanites is an Upper Coniacian to Santonian genus (Wright 1957; Toshimitsu 1988), which may be present in the Middle Santonian of Angola.

Genus *Texanites* Collignon, 1948

Type species

Ammonites texanus Roemer, 1852; by original designation.

Texanites venustus Collignon, 1948
Figs 7A–B, 8A–G, 9A

1948	*Texanites venustus* Collignon, p. 81, pl. 9 (fig. 4).
1966	*Texanites venustus* Collignon, p. 74, pl. 484 (fig. 1960).

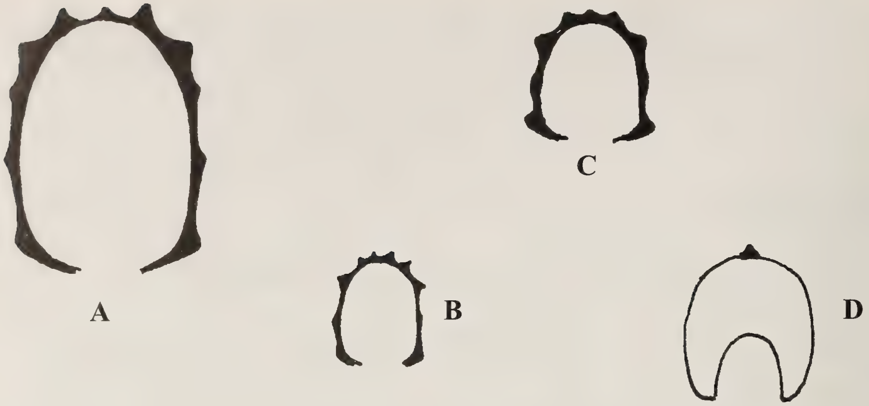

Figure 7

Whorl sections. × 1. A–B. *Texanites venustus* Collignon. A = SAM–PCA1992, B = SAM–PCA1967. C. ?*Protexanites* sp., SAM–PCA2015. D. *Damesites sugata* (Forbes).

1980 *Texanites venustus* Collignon; Klinger & Kennedy, p. 124.

Material

Thirty-three specimens, the majority very fragmentary, including SAM–PCA1718, 1967, 1972–73, 1978, 1982, 1986, 1992, 1994, 1998, 2001, 2009, 2013, 2019, 2024, 2030–31, 2037, and 2048, with both recrystallized test preserved and internal moulds.

Description

The shell is strongly compressed, very evolute, with *c.* 20 per cent of the penultimate whorl covered. The umbilicus is very wide (38–47% of the shell diameter) and shallow, with a subvertical wall and evenly rounded shoulder. The whorl section (Fig. 7A–B) is compressed (H/W = 1.09–1.44), elliptical intercostally and polygonal costally, with broad, flat flanks and a narrow venter bearing a low well-developed siphonal keel. Maximum width is just below midflank. Ribs begin at the umbilical seam and pass radially outwards to prominent umbilical bullae, of which there are 22–24 per whorl. These give rise singly, or in pairs, to 38–44 strong prorsiradiate ribs per whorl; where single there is generally an associated intercalatory. On relatively large whorl fragments the majority of ribs seem to be single and slightly convex adorally across the flank, suggesting a simplification of ribbing in maturity. From the earliest stage visible flank costae are ornamented with a prominent rounded tubercle just below midflank, closely spaced marginal and submarginal clavi, and strongly clavate external tubercles. The latter are separated from the low siphonal keel by shallow sulci.

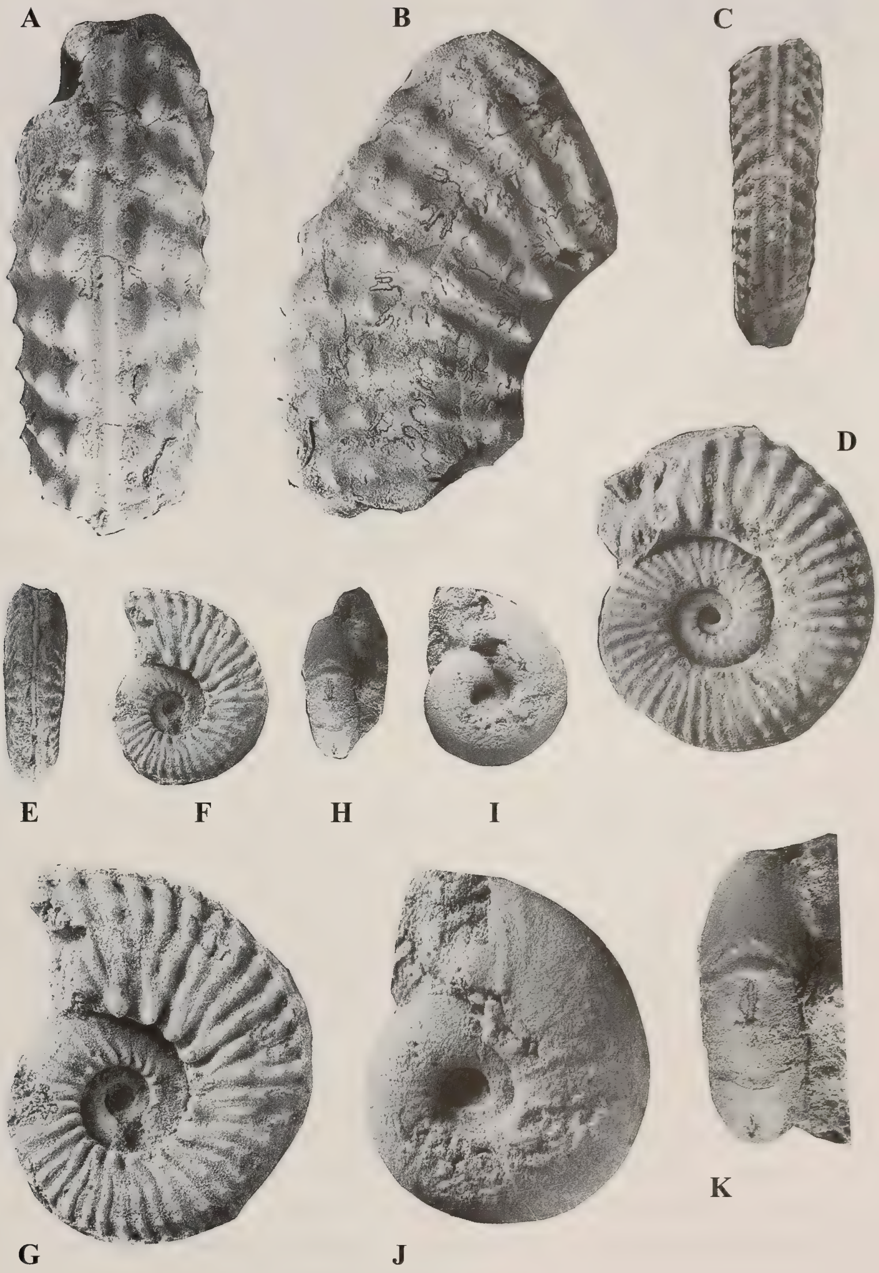

Figure 8

A–G. *Texanites venustus* Collignon. A–B. Ventral and lateral views of SAM–PCA1992. C–D. Ventral and lateral views of SAM–PCA1967. E–F × 1; G × 2. H–K. *Menuites* sp. juv. H–I. Ventral and lateral views of SAM–PCA2016. × 1. J–K. Same. × 2.

Material

Specimen	D	H	W	H/W	U
SAM–PCA2019	24	10 (0.42)	8 (0.33)	1.25	10 (0.42)
SAM–PCA2048	*c.* 24	9 (0.38)	7 (0.29)	1.29	*c.* 11 (0.46)
SAM–PCA2030	25	10 (0.40)	9(0.36)	1.11	10 (0.40)
SAM–PCA1982	31	11 (0.35)	9 (0.29)	1.22	14 (0.45)
SAM–PCA1998	32	12 (0.38)	11 (0.34)	1.09	15 (0.47)
SAM–PCA1718	36	14 (0.39)	?	?	17 (0.47)
SAM–PCA2001	*c.* 43	15 (0.35)	?	?	18 (0.42)
SAM–PCA1967	43	15 (0.35)	12 (0.28)	1.25	17 (0.40)
"	34	13 (0.38)	10 (0.29)	1.30	13 (0.38)
SAM–PCA1978	47	16 (0.34)	13 (0.28)	1.23	20 (0.43)
"	31	12 (0.39)	9 (0.29)	1.33	13 (0.42)
SAM–PCA1994	*c.* 65	23 (0.35)	18 (0.28)	1.28	*c.* 28 (0.43)
SAM–PCA2009	?	36	27	1.33	?
SAM–PCA1992	?	36	25	1.44	?

Discussion

The Angolan material conforms well with descriptions of the Madagascan material (Collignon 1948, 1966) and is considered to be conspecific. Other texanites to be described from Angola are *T. angolanus* Haas (1942: 12, figs 8–10), *T. angolanus berryi* Haas (1942: 15, fig. 11) and *Texanites quinquenodosus evolutus* (Haas 1942: 18, fig. 12). The former two have been included (Cooper 1989) in the synonymy of *T. roemeri* (Yabe & Shimizu) (Young 1963: 84, pl. 43 (fig. 1), characterized by coarse single ribs, and the latter taxon differs from the present species in being serpenticone (umbilicus 63% of shell diameter).

Of species that warrant comparison, *Texanites dichotomus* Collignon (1948: 80, pl. 9 (fig. 3), pl. 11 (fig. 1)) has similar ornament but typically depressed whorls (H/W = 0.83–0.91). Among the south-east African material described by Klinger & Kennedy (1980), the Angolan material is closest to highly variably *T. soutoni* (Baily, 1855: pl. 11 (fig. 1)); *Texanites soutoni natalensis* Klinger & Kennedy (1980: 214, figs 164–185) is based on much larger specimens that are difficult to compare but seem to be more evolute, with fewer (24–38) ribs per whorl. *Texanites soutoni soutoni* (Baily) (Klinger & Kennedy 1980: 189, figs 143–151, 152B, 153–163) has similar proportions but, at comparable diameters to the Angolan material, lacks bifurcating ribs. *Texanites umzambiensis* Klinger & Kennedy (1980: 167, figs 126–129, 152A) has lower whorls (whorl height only 30% of the diameter), inner whorls with prominent ventrolateral spines, and fewer, generally simple ribs per whorl.

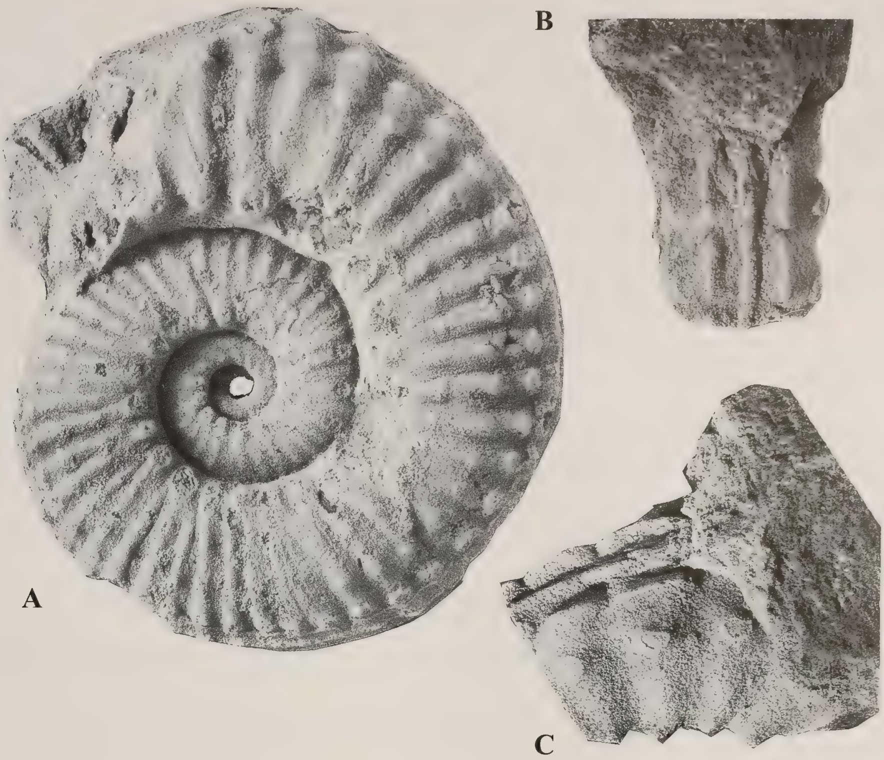

Figure 9

A. *Texanites venustus* Collignon. × 2. Lateral view of SAM–PCA1967. B–C. ?*Protexanites* sp. × 1.5. Ventral and lateral views of SAM–PCA2015.

American *T. americanus* (Lasswitz) (Young 1963: 83, pl. 41 (figs 1, 3), pl. 44 (figs 2–3), pl. 48 (figs 1, 3), pl. 57 (fig. 5), text-fig 24c) has only 12–19 ribs per whorl at diameters below 50 mm, whereas very similar *T. shiloensis* Young (1963: 89, pl. 46 (figs 1–4), pl. 54 (figs 4–7), pl. 70 (figs 5–6, 8), text-fig. 24d) has only 7–8 intercalatory ribs at diameters of 40 mm or less and weaker tuberculation. *Texanites lonsdalei* Young (1963: 90, pl. 34 (fig. 1), pl. 51 (figs 3–7), pl. 58 (figs 5–6), text-fig. 22a, d) is more involute than the present species, with fewer, generally simple costae.

Occurrence

Texanites venustus Collignon is known only from the Middle Santonian of Madagascar (Collignon 1966) and now Angola.

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ANNALS OF THE SOUTH AFRICAN MUSEUM

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OBSERVATIONS ON THE SYSTEMATICS, GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION AND ORIGIN OF *DIPLOMOCERAS CYLINDRACEUM* (DEFRANCE, 1816) (CEPHALOPODA: AMMONOIDEA)

by

HERBERT CHRISTIAN KLINGER

&

WILLIAM JAMES KENNEDY

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(With 17 figures)

[*MS accepted February 2003*]

ABSTRACT

The heteromorph ammonite genus *Diplomoceras* has a near world-wide distribution in the Maastrichtian, but records as far back as early Campanian have been quoted. Due to the generally fragmentary nature of the material and intraspecific variation, systematics of the genus are disputed. According to recent comprehensive reviews by Kennedy (1986*a*, 1987 *et seq.*), the genus appears to be monospecific, consisting of the type species, *Diplomoceras cylindraceum* (Defrance, 1816) only. Differential preservation of internal moulds of the phragmocone and body chamber respectively, and similarities in suture lines suggest that the origins of *Diplomoceras cylindraceum* may be sought in *Neoglyptoxoceras annulatum* (Collignon, 1969), a species thus far known only from the lower Campanian of Madagascar.

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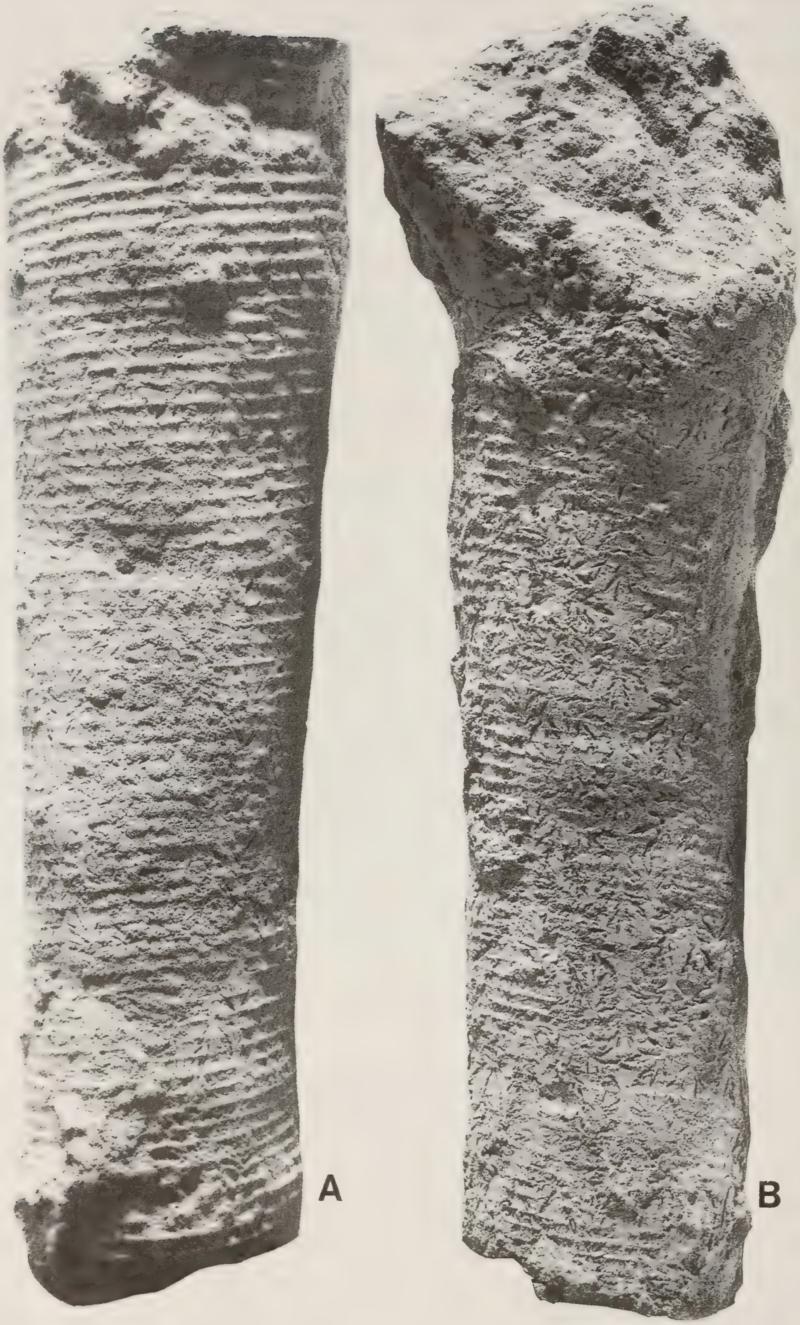

Figure 1

Diplomoceras cylindraceum (Defrance, 1816). SAM–PCZ9551 from locality 113, KwaZulu, St Lucia Formation. Maastrichtian a or b. An internal mould that retains the ribbing. × 1.

INTRODUCTION

The heteromorph ammonite *Diplomoceras cylindraceum* (Defrance, 1816), type species of the genus *Diplomoceras* Hyatt, 1900, is a conspicuous faunal element of the Maastrichtian stage by virtue of its near-cosmopolitan distribution, paper clip-like coiling and, in some instances, gigantic size. It is also amongst the last surviving ammonites before the demise of the Order Ammonoidea at the end of the Cretaceous Period.

Diplomoceras typically consists of several straight shafts, connected by a series of variable U-shaped sections (Figs 1–6). Because of this loose coiling, post-mortem fragmentation is universal and complete specimens of the species are unknown. The early whorls were thought to have been coiled in a helix (cf. Wright 1957: L227; Matsumoto 1959: 165; Klinger 1976: 81), but this misconception was probably based on a helically coiled heteromorph from Seymoũr Island, Antarctic Peninsula, described and figured as *Anisoceras (Diplomoceras) notabile* Whiteaves, 1903 by Kilian & Reboul (1906: 15 (*pars*), pl. 5, pl. 6 (fig. 1) only). These specimens are definitely not conspecific with *D. notabile*, and may possibly be *Nostoceras* (*Bostrychoceras*) *sanctaeluciense* Klinger, 1976, but without having seen the actual specimens we can not be sure. Juvenile specimens tentatively referred to *D. notabile* by Matsumoto (1984: 312, pl. 8 (fig. 3)) and Matsumoto & Miyauchi (1984: 68, pl. 27 (fig. 2); text-fig. 11A) suggest that the paper clip-like coiling already occurs from a very early ontogenetic stage. Gigantic specimens with estimated total uncoiled lengths of *c.* 2.5 metres have been recorded from Seymour Island as *Diplomoceras maximum* Olivero & Zinsmeister (1989: 629, figs 2.5, 4.1–4.4, 5.1–5.4), exceeding in size by far the largest late Cretaceous (straight) baculitids (see Klinger & Kennedy 2001). Up to now, no complete specimen has been found, and the adult aperture is unknown.

The whorl section is generally circular, or slightly compressed or depressed (Fig. 2E). Ornament on the shell consists of simple, uniform ribs with no tubercles (Figs 5–6). Constrictions, if present (cf. Henderson *et al.* 1992, fig. 5A–B; Kennedy 1999: 653, fig. 12.1–2) are rare. On internal moulds, however, ornament differs between the phragmocone and body chamber. Internal moulds of the phragmocone are usually (Figs 2B, 3–4), but not always (Figs 1, 2A, C–D) smooth whereas internal moulds of the body chamber retain the ribbing. This conspicuous anomaly has been noted on several occasions (see Olivero & Zinsmeister 1989: 627; Henderson *et al.* 1992: 141; Kennedy 1999: 657), and according to Olivero & Zinsmeister (1989), can be ascribed to the thickening of the nacreous shell layer below the ribs on the phragmocone, and may be considered diagnostic of the genus *Diplomoceras*. Apart from shell structure, the latter authors also provided details of muscle scars, previously recorded by Jones (1961), and speculated on the mode of life and buoyancy control of *Diplomoceras*. The suture line (Fig. 7A–C) is deeply incised with a large bifid lateral (*L*) and umbilical (*U*) lobe, and a small, trifid internal (*I*) lobe. The saddles all have very narrow stems.

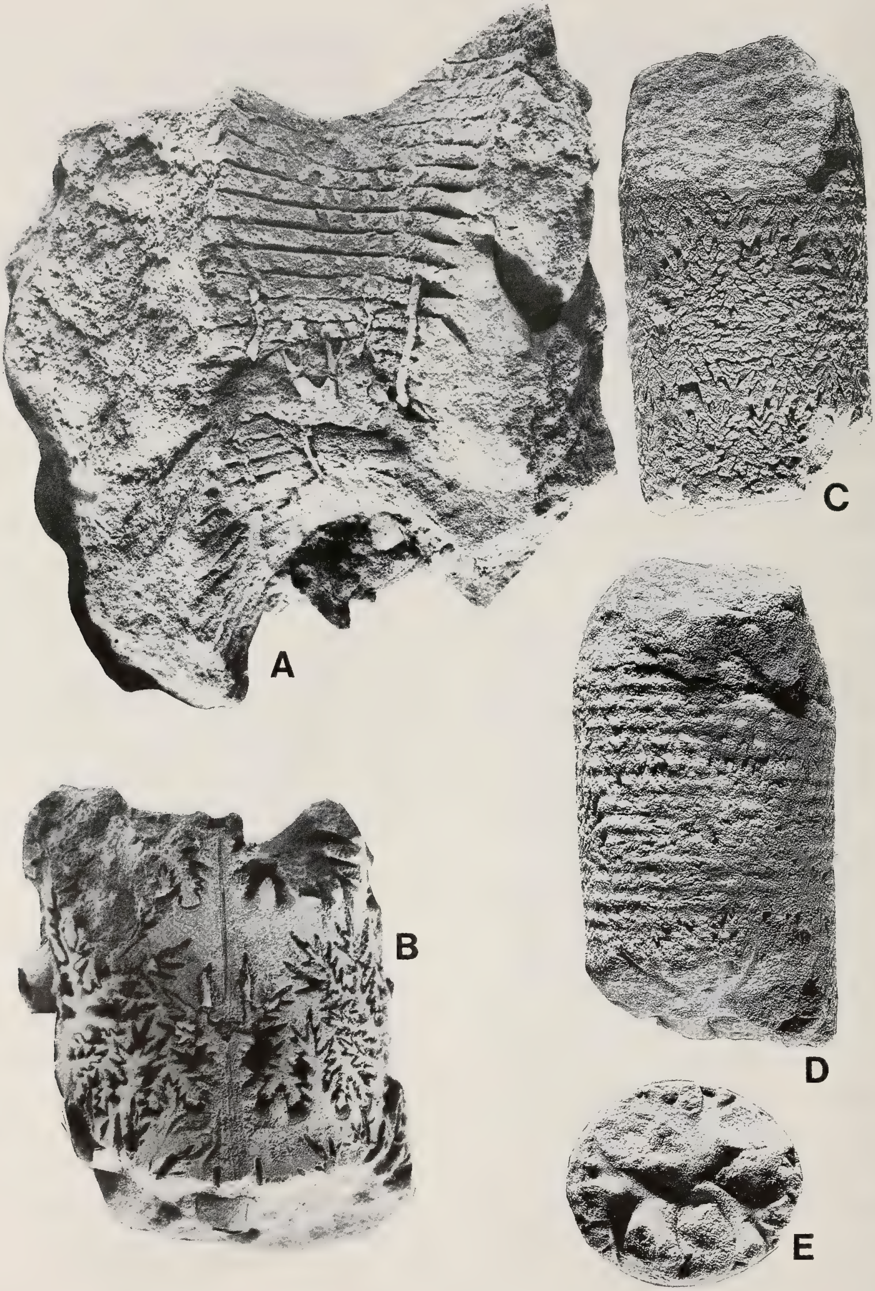

Figure 2

Diplomoceras cylindraceum (Defrance, 1816). A. SAM–PCZ7940 from locality 20, KwaZulu, St Lucia Formation. Maastrichtian a or b. B. SAM–PCZ7904 from the same locality as A. C–E. SAM–PCZ17356 (ex H105/9) from locality 116, KwaZulu, St Lucia Formation, Maastrichtian a. All × 1.

SYSTEMATICS

The geographic and stratigraphic distribution of the genus *Diplomoceras* is largely dependant on whose taxonomic procedure is followed. Conservatively, the following species have been referred to the genus with differing degrees of confidence:

1. *D. cylindraceum* (Defrance, 1816)—the type species.
2. *D. notabile* Whiteaves, 1903.
3. *D. lambi* Spath, 1953.
4. *D. maximum* Olivero & Zinsmeister, 1989.
5. *D. australe* Hünicken, 1965.

Apart from these, several species from California have been attributed to the genus by Anderson (1902, 1958), but these are either uninterpretable from the figures and descriptions, or are synonyms of the above.

Kennedy (1987), in his revision of the ammonite fauna of the type Maastrichtian, and subsequently (Kennedy & Henderson 1992; Henderson *et al.* 1992), based on Indian and Western Australian material respectively, regard *D. notabile*, *D. lambi* and *D. maximum* as junior synonyms of *D. cylindraceum* because of overlapping dimensions of the whorl section and density of ribbing.

Based on the compressed whorl section (Wb:Wh = 1,26 and 1,24) of the holotype, the only other species that may be referable to the genus according to these authors is *D. australe*. However, according to Macellari (1986: 9), the specimens referred to this species by Hünicken appear to be deformed, and may be referred to *D. lambi*, that is, *D. cylindraceum* as interpreted by Kennedy (1987, and subsequent discussions).

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

If the taxonomic procedure of Kennedy (1986*a*, 1987 *et. seq.*) is accepted, the genus *Diplomoceras* is monospecific, comprising the type species, *D. cylindraceum* (Defrance, 1816) only.

Diplomoceras cylindraceum has a near world-wide distribution (Figs 8–9), being most common in high northern and southern latitudes, but is remarkably rare in equatorial regions and is apparently absent from the Middle East (Zeev Lewy pers. comm.) and Angola and Nigeria. It ranges throughout the whole of the Maastrichtian stage.

There are, however, earlier, Campanian records of *D. cylindraceum*, some apparently extending back to the early Campanian (Alabushev & Wiedmann 1997). Upper Campanian records from Japan include those of Matsumoto & Morozumi (1980), Matsumoto (1984) and Matsumoto & Miyauchi (1984). In Zululand (Klinger & Kennedy, this volume 110(6), p. 303) *D. cylindraceum* occurs mainly in the Maastrichtian, but a single specimen is known from the uppermost Campanian of Kennedy & Klinger's (1975) locality 111 (Klinger & Kennedy, this volume 110(6), p. 303). In Antarctica, the species has been dated as late Campanian–early Maastrichtian and late Maastrichtian as *D. lambi* and *D. maximum* respectively. In northern Spain, Gallemi *et al.* (1983) have records of *D. notabile* from the upper Campanian. Machalski (1996) also tentatively records

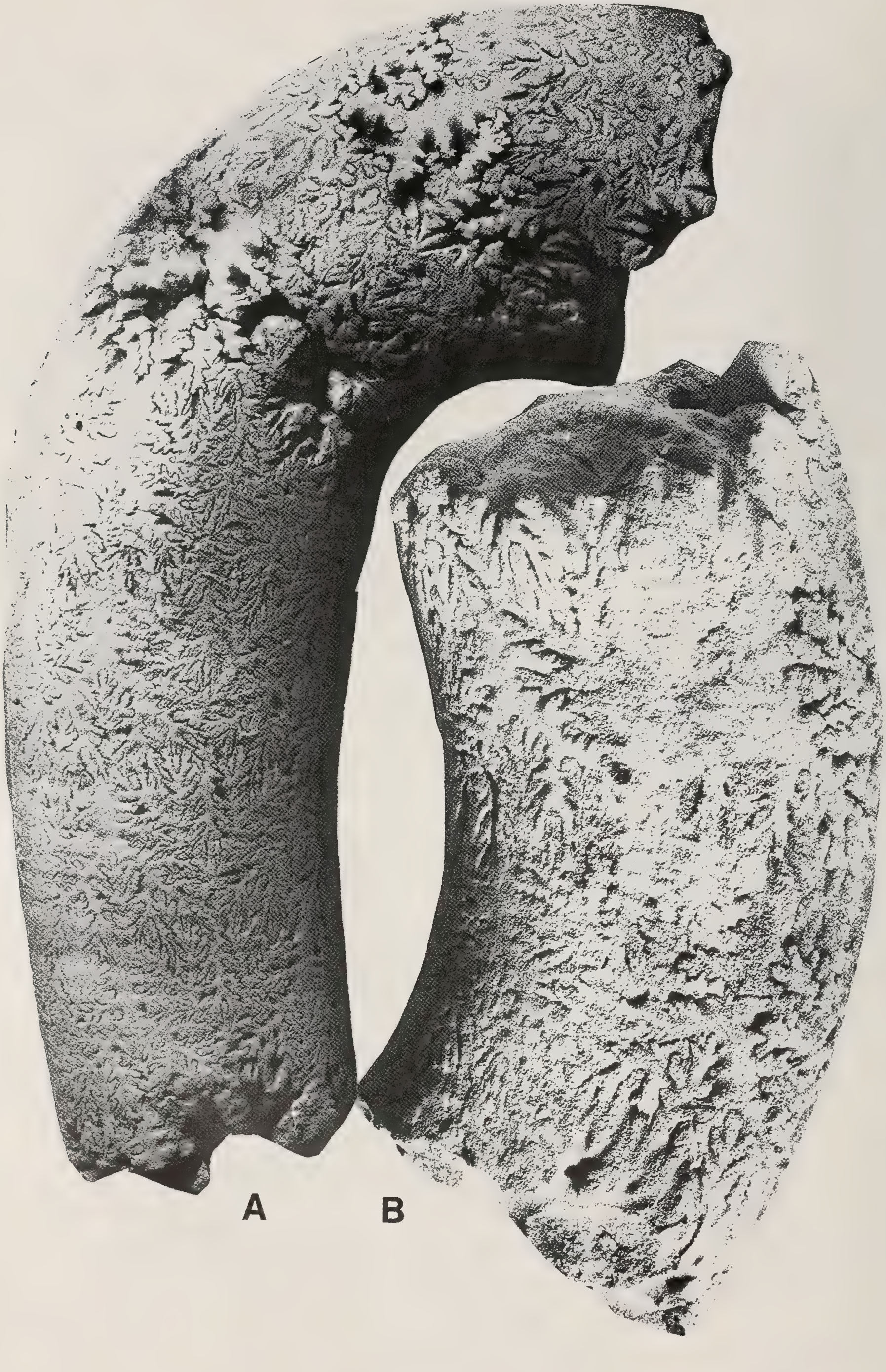

Figure 3

Diplomoceras cylindraceum (Defrance, 1816). A. IRSNB 10292 ex Ubaghs Collection from the upper Maastrichtian Calcaire de Kunraed of Kunrade, Limburg, The Netherlands. B. IRSNB 10262 (IG 8261 ex De Jaer Coll.) from the same horizon and locality as A.

D. cylindraceum from the upper Campanian of the Piotrawin section in Central Poland. Küchler & Odin (2001) also record *D. cylindraceum* from the upper Campanian of Tercis, France.

The stratigraphic distribution of the species in southern Sakhalin reported by Alabushev & Wiedmann (1997) is difficult to interpret. According to these authors, *D. cylindraceum* s.s. is restricted to the upper Maastrichtian and is the index fossil for the eponymous zone as proposed by them for northeast Russia. *Diplomoceras notabile*, on the other hand, is reported (Alabushev & Wiedmann 1997: 15) to occur in the lower Campanian of Sakhalin and the lowermost Campanian of northwestern Kamchatka but, according to their Table 1 (p. 29) occurs throughout the whole of the Campanian. The specimen figured as being from the lower Campanian (Alabushev & Wiedmann 1997, pl. 4 (fig. 1)) is part of a juvenile shell, and is generically indeterminable; it could be referred to either *Diplomoceras* or *Glyptoxoceras*.

Even if the record of the first occurrence of *D. cylindraceum* in the lower Campanian is incorrect, its definite occurrence from the upper Campanian to the end of the Maastrichtian makes it one of the longest ranging heteromorph ammonite species of the Cretaceous Period.

ORIGIN OF *DIPLOMOCERAS CYLINDRACEUM*

Despite its near-cosmopolitan occurrence and long stratigraphic range, the origins of the species and genus have received little attention. Matsumoto & Miyauchi (1984: 68) suggested an origin in *Scalarites* (together with *Glyptoxoceras*), but no further details were given.

Based on similarities in suture lines, mode of coiling, ornamentation in general, and differences in ornament on internal moulds of the phragmocone and body chamber respectively, we suggest an origin for *Diplomoceras cylindraceum* in the poorly known and apparently endemic material from Madagascar referred to the two genera, *Neoglyptoxoceras* Collignon, 1969 and *Epiglyptoxoceras* Collignon, 1969. *Neoglyptoxoceras*, type species *Neoglyptoxoceras magnificum* Collignon, 1969 (1969:30, pl. 523 (fig. 2065), p. 35, pl. 526 (figs 2074–2075)) (Fig. 10A–B) and *Epiglyptoxoceras*, type species *Epiglyptoxoceras abnorme* Collignon, 1969 (1969: 35, pl. 526 (fig. 2076)) are both relatively common in the lower Campanian of Madagascar. Apart from the type species, *Neoglyptoxoceras* is further represented by *N. perangustum* Collignon, 1969 (1969: 38, pl. 527 (fig. 2078)) (Fig. 11) and *Epiglyptoxoceras* by *E. annulatum* Collignon, 1969 (1969: 41, pl. 529 (fig. 2083)) (Figs 12–15) and *E. giganteum* Collignon, 1969 (1969: 40, pl. 528 (figs 2081–2082)) (Fig. 16) in the lower Campanian. *Neoglyptoxoceras* persists to the middle Campanian of Madagascar as *Neoglyptoxoceras serta* Collignon, 1970 (1970: 15, pl. 613 (figs 2286–2289)) (*non* Müller & Wollemann, 1906). As their names indicate, *Neoglyptoxoceras* and *Epiglyptoxoceras* are superficially similar to the genus *Glyptoxoceras* Spath, 1925 in being ornamented by ribs only, but differ from that genus in their much larger size.

According to Collignon, the two genera differ from each other in the number of saddles and lobes in their suture lines. *Neoglyptoxoceras* was reported to have four saddles instead of three, and three lobes instead of two as in *Epiglyptoxoceras*.

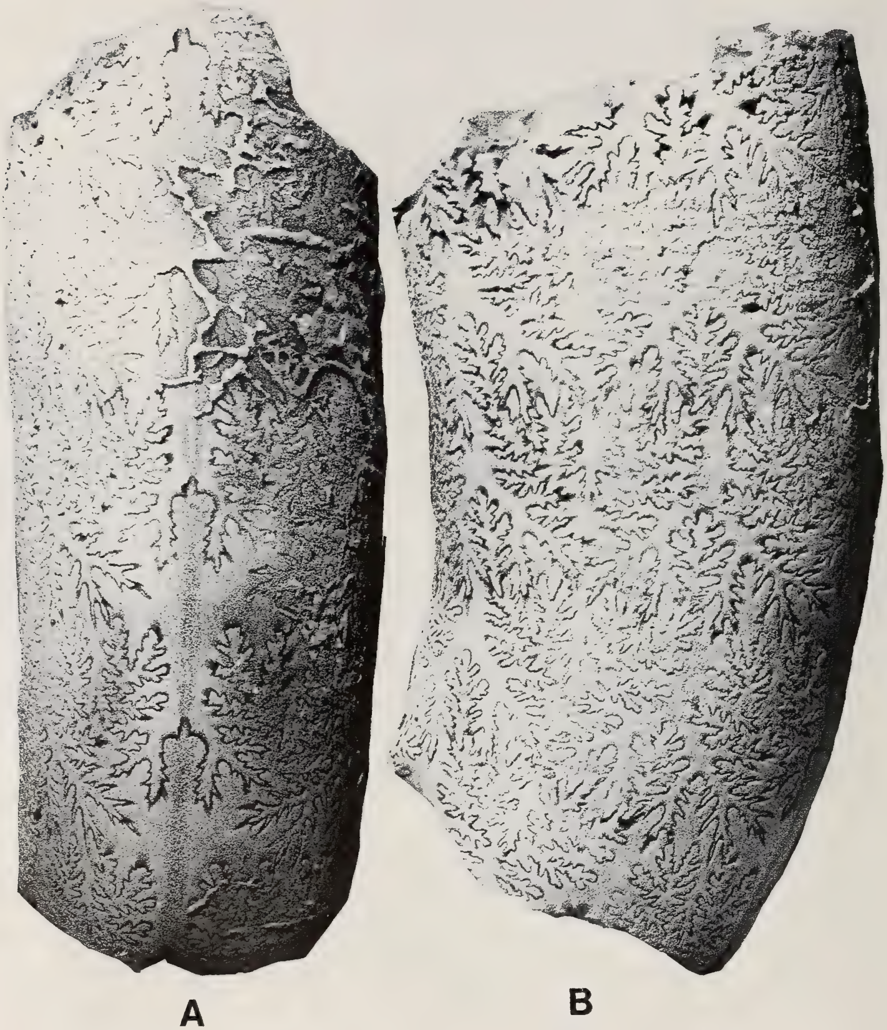

Figure 4

Diplomoceras cylindraceum (Defrance, 1816). IRSNB 10257 (IG 6521 ex Ubaghs Collection) from the upper Maastrichtian Calcaire de Kunraed of Kunrade, Limburg, The Netherlands. × 1.

Unfortunately, Collignon's sutural terminology is confusing and needs to be clarified. According to the sutural terminology of Wedekind (1916), reviewed by Kullmann & Wiedmann (1970), the adult suture of Cretaceous heteromorph ammonites consists of four lobes, *E* (External), *L* (Lateral), *U* (Umbilical) and *I* (Internal); the three saddles are referred to by their positions relative to the lobes, i.e. *E/L, L/U, U/I.*

The following is Collignon's original diagnosis of *Neoglyptoxoceras* (1969: 35) with our interpretation of the sutural terminology in parenthesis.

"...et surtout par sa cloison qui compte 4 selles au lieu de 3, et 3 lobes au lieu de 2. Ces 4 selles sont de forme careé, avec lobule médian plus ou moins oblique. Le premier lobe (*L*) très étalé, très volumineux, deux fois plus long que le siphonale (*E*); le deuxième (a large median incision of the saddle *U/L*) est réduit, en forme d'étoile; le troisième (*U*) présqu'aussi fort et long que le premier, présente une branche externe prépondérante. Lobule antisiphonal (*I*) très alloñgé".

The "extra" lateral lobe in *Neoglyptoxoceras* is in fact no more than a large, median incision of the saddle *L/U*, which is very broad. In *Epiglyptoxoceras*, this saddle *(L/U*) is constricted at the base, and the median incision is reduced (compare Collignon 1969, figs 2074–2076, 2081–2083). This suture pattern differs in no significant respects from that of *D. cylindraceum* (See Fig. 7). We agree with Wright (1997: L250) in regarding *Epiglyptoxoceras* as a synonym of *Neoglyptoxoceras*, albeit for different reasons; Wright considered *Epiglyptoxoceras* to be based on a pathological specimen. We do not think that the sutural differences between the type species of the two taxa merit separation at generic level, and as first revising authors select the name *Neoglyptoxoceras* for the taxon.

Apart from similar sutures, *Neoglyptoxoceras* resembles *Diplomoceras* in being ornamented by ribs only. A further, and in our consideration, crucial similarity is in the difference in ornament between internal moulds of the phragmocone and body chamber in both *Diplomoceras* and *Neoglyptoxoceras*. It is well known that internal moulds of *D. cylindraceum* are generally smooth, whereas the same mode of preservation of the body chamber produces distinct ribbed ornament. This anomaly has been ascribed to abnormal thickening of the middle nacreous layer below the ribbing on the phragmocone, and is considered characteristic of the genus *Diplomoceras* by Olivero & Zinsmeister (1989: 627, with additional references). A similar, though not identical situation exists in *Neoglyptoxoceras*. Here, ribbing occurs on both phragmocone and body chamber, but the strength and shape of ribbing changes dramatically on internal moulds at the end of the phragmocone and beginning of the body chamber. This can be clearly seen on the holotype and paratype of *N. magnificum* (Collignon 1969, pl. 523 (fig. 2065); pl. 526 (figs 2074–2075)) (Fig. 10A–B); see also Fig.17). Similar differences in ribbing on the body chamber and phragmocone on internal moulds have also been recorded in *Glyptoxoceras rugatum* by Henderson *et al.* (1992) and may possibly be a diagnostic feature of some of the genera referred to the subfamily Diplomoceratinae Spath, 1926.

The ribbing of *Neoglyptoxoceras magnificum* is too coarse, and the suture line a little too different for it to be considered directly ancestral to *D. cylindraceum.* The fine ribbing of *Neoglyptoxoceras annulatum* (Collignon, 1969) (Collignon 1969: 41, pl. 529 (figs 2083–2084)) (see also Figs 12–15), however, is perfectly compatible with that of

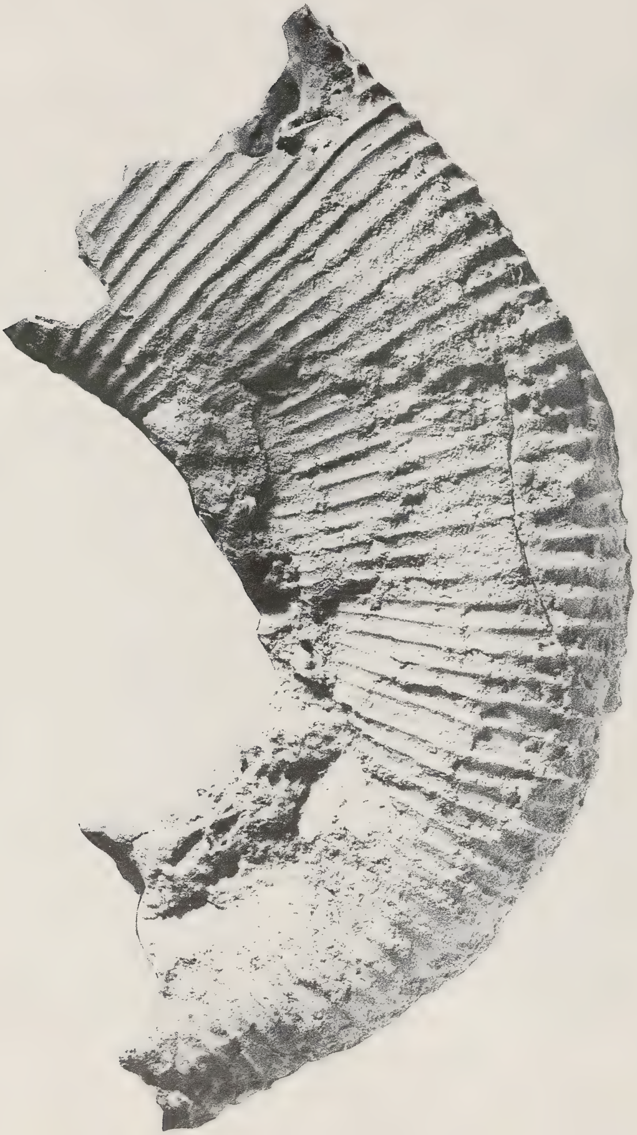

Figure 5

Diplomoceras cylindraceum (Defrance, 1816). IRSNB 10290, ex Ubaghs Collection from the upper Maastrichtian Calcaire de Kunraed of Kunrade, Limburg, The Netherlands. The specimen retains silicified shell. × 1.

D. cylindraceum. In addition, the coiling in *N. annulatum* changes from crioconic in the early stages of growth (Fig. 15) to more elliptical, tending towards straightening of the shaft in the adult stage (Figs 12–14). In fact, some specimens of *N. annulatum* (Figs 13–14) and *D. cylindraceum* (Kennedy 1987, pl. 23 (fig. 1)) (Fig. 3A) have near-identical coiling. In addition, in larger specimens of *N. annulatum* the whorl section changes from slightly compressed at the smaller adapical end to near-circular at the larger abapertural end.

A curious feature of *N. annulatum* is that successive sutures, rather than interdigitating as in *D. cylindraceum*, are clearly separated, producing smooth zones on the internal mould (Figs 12A–B, 13–14). As yet, we have no explanation for this distinctive feature, but similar, widely-spaced sutures also occur in *Glyptoxoceras* cf. *subcompressum* (Forbes 1846) (Kennedy 1987: 179, pl. 26 (figs 1–6, 8–9, 13–14, 19–21)) from the upper Maastrichtian of Kunrade, The Netherlands.

We believe that all the necessary elements for the "Bauplan" of *D. cylindraceum* may be found in *N. annulatum*. Apart from the smooth band between successive sutures, these elements include similar suture lines, the change in ornament on internal moulds from the phragmocone to the body chamber, the adult whorl section, and progressive tendency towards elliptical coiling on the outer whorl, eventually leading towards the straight limbs of *D. cylindraceum*. With the exception of a single possible specimen from KwaZulu (Fig. 10C) the genus *Neoglyptoxoceras* appears to be endemic to Madagascar. Previous records of *Neoglyptoxoceras* from Europe, e.g. (*Neoglyptoxoceras* (?) *retrorsum* in Kennedy 1986*b:* 106, pl. 16 (figs 1–4, 6–7); pl. 17 (figs 1–2); text-fig. 38) are best referred to *Glyptoxoceras*.

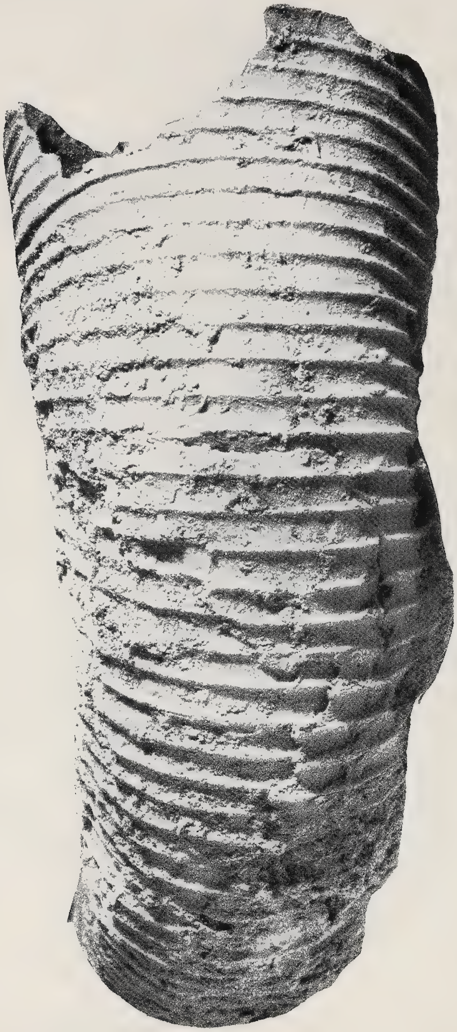

Figure 6

Diplomoceras cylindraceum (Defrance, 1816). IRSNB 10290, ex Ubaghs Collection from the upper Maastrichtian Calcaire de Kuraed of Kunrade, Limburg, The Netherlands. The specimen retains silicified shell. × 1.

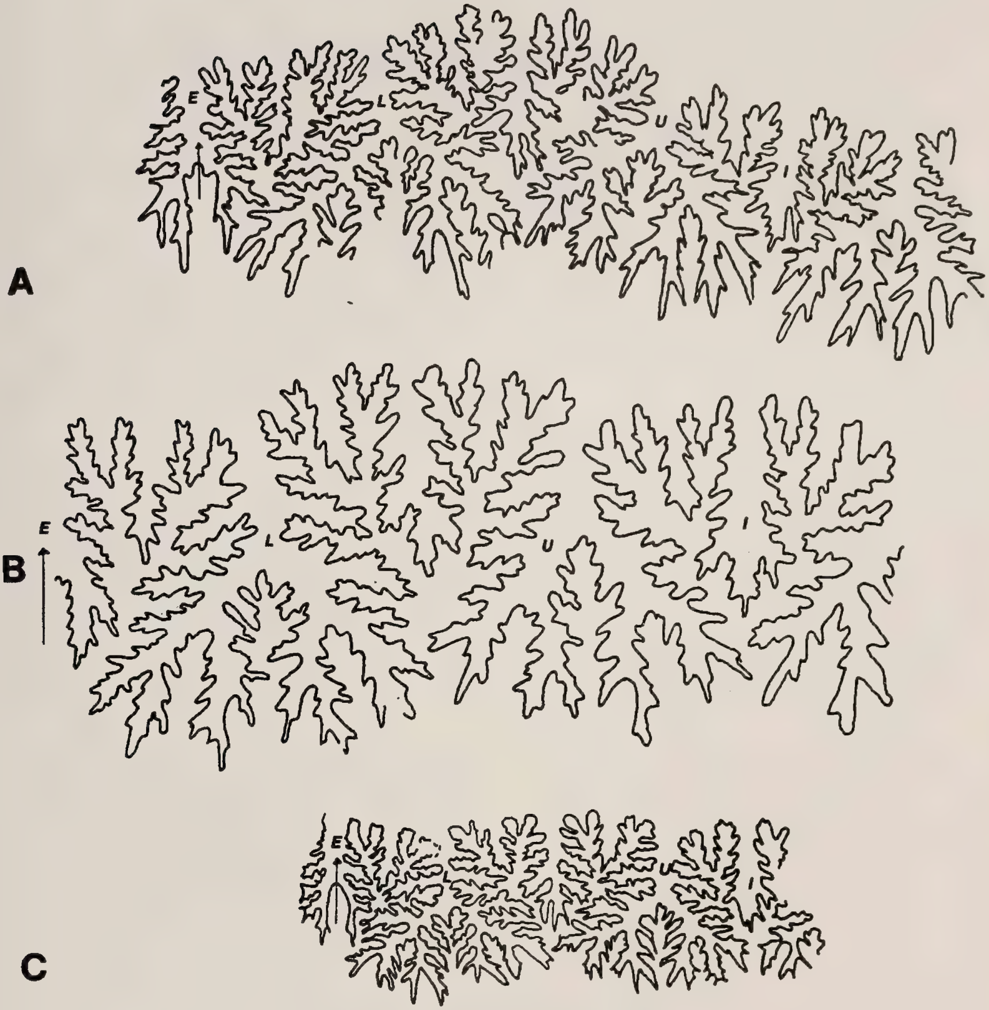

Figure 7

Suture line of *Diplomoceras cylindraceum* (Defrance, 1816). A. Copy after Kennedy 1986*a*, text-fig. 7M. B. Copy after Macellari 1986, fig. 15. C. Copy after Jones 1963, fig. 15.

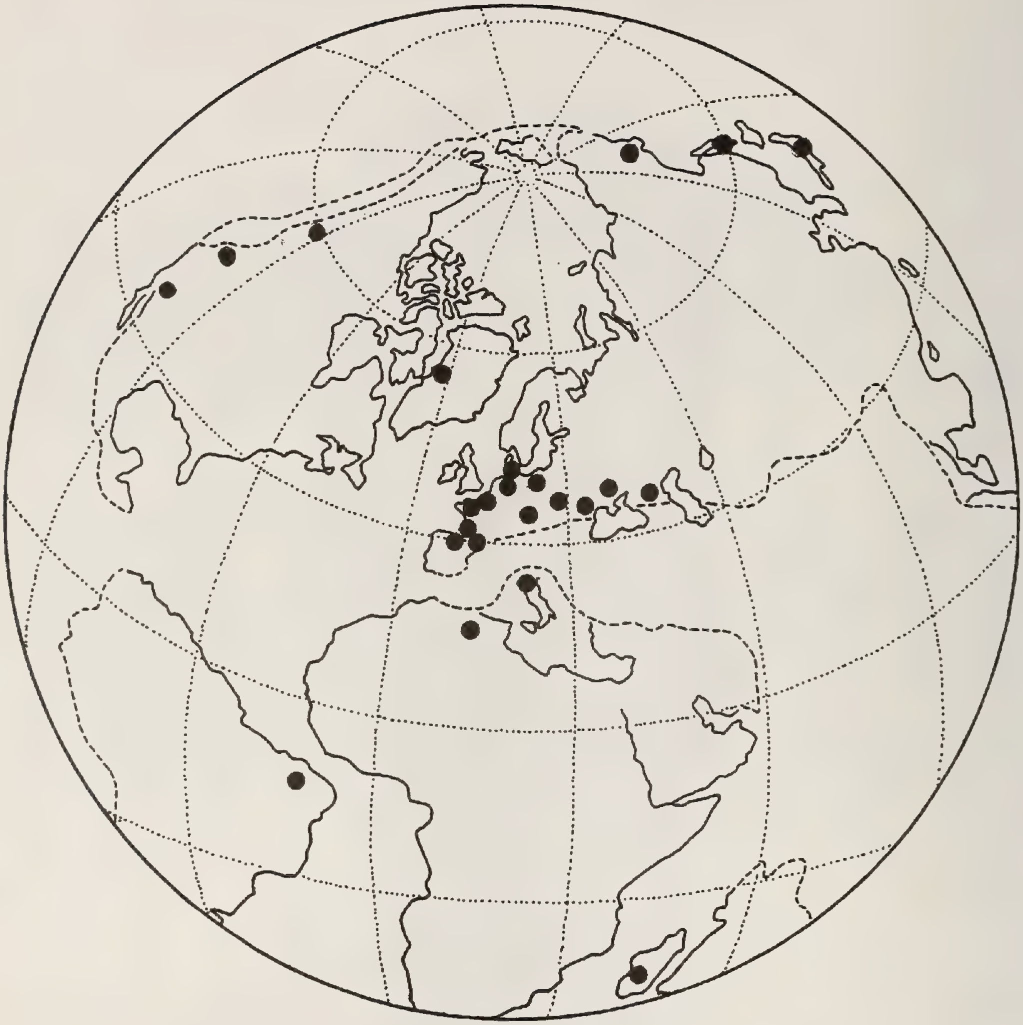

Figure 8 above (and see Figure 9)

Geographic distribution of *Diplomoceras cylindraceum* (Defrance, 1816). France, Biscay Region (Ward & Kennedy 1993), Pyrénées Atlantiques (Kennedy 1986*c*), Tercis (Küchler & Odin 2001); Cotentin Peninsula (Kennedy 1986*a*); Northern Spain (Wiedmann 1962); Italy (Mariani, 1898); The Netherlands (Kennedy 1987); Belgium, the Mons Basin (Kennedy 1993); northern Germany (Schlüter 1872); Denmark (Birkelund 1993); Poland (Blaszkiewicz 1980; Machalski 1996); Austria (Kennedy & Summesberger 1986); The Ukraine (Kennedy & Summesberger 1987); Bulgaria (Tzankov 1982); Serbia (ex Yugoslavia) (Petkovic 1953); Don Basin, Russia (Naidin 1974); Caucasus & Crimea (Naidin & Shimanskij 1959); European Russia (Mikhailov 1951); Arctic Siberia (Dundo 1971);

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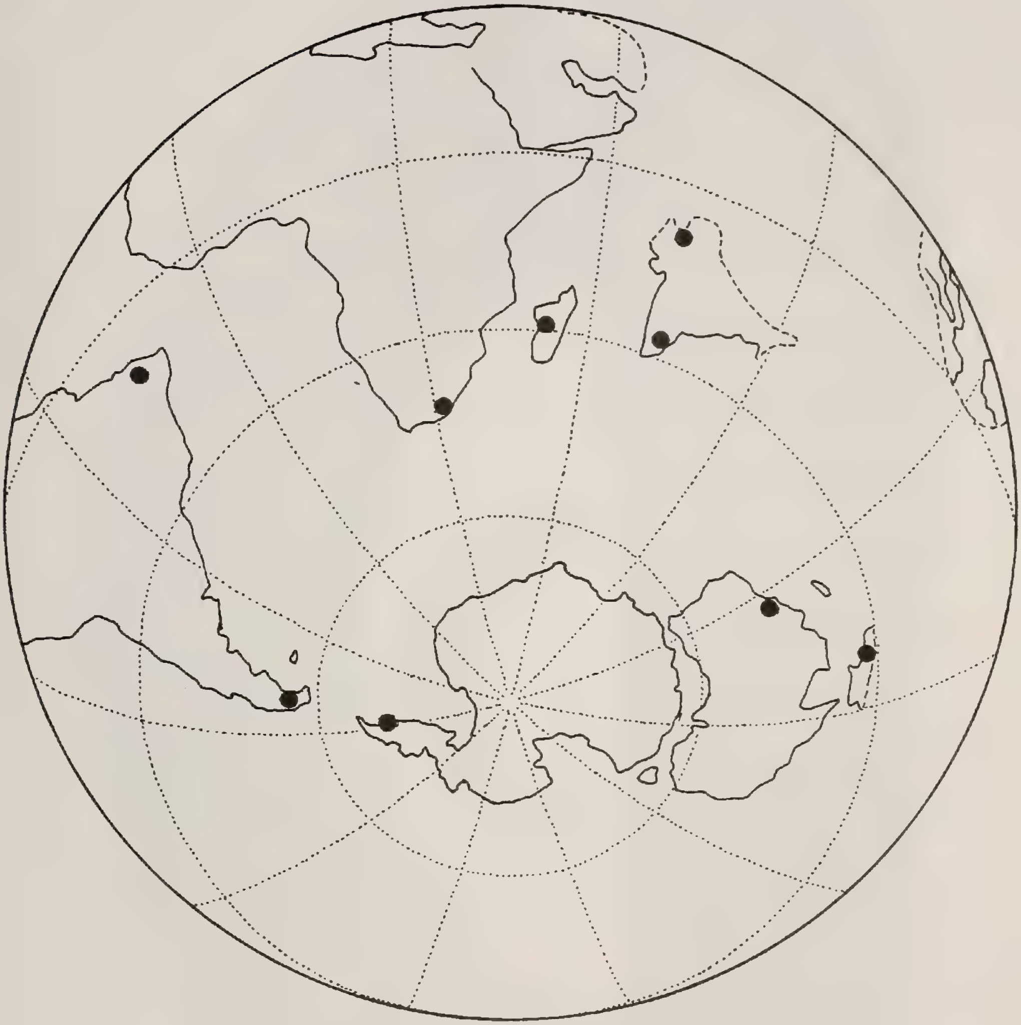

Figure 9

Continued from previous page:

Northwestern Kamchatka & southern Sakhalin (Alabushev & Wiedmann 1997); Tunisia (Robaszynski *et al.* 2000); South Africa (KwaZulu) (Klinger 1976); Madagascar Collignon 1971); South India (Kennedy & Henderson 1992); Pakistan, Baluchistan (Kennedy 1999 *in* Fatmi & Kennedy); Western Australia (Henderson *et al.* 1992); Antarctic Peninsula (Olivero & Zinsmeister 1989); Argentina (Hünicken 1965); Chile (Stinnesbeck 1986); Brazil (Maury 1930); California (Anderson 1902, 1958); British Columbia (Whiteaves 1903); Alaska (Jones 1963); Japan, Hokkaido (Matsumoto 1984); and possibly West Greenland (Birkelund 1965) and New Zealand (Henderson 1970). This list is not intended to be complete, and references are mainly restricted to one per locality.

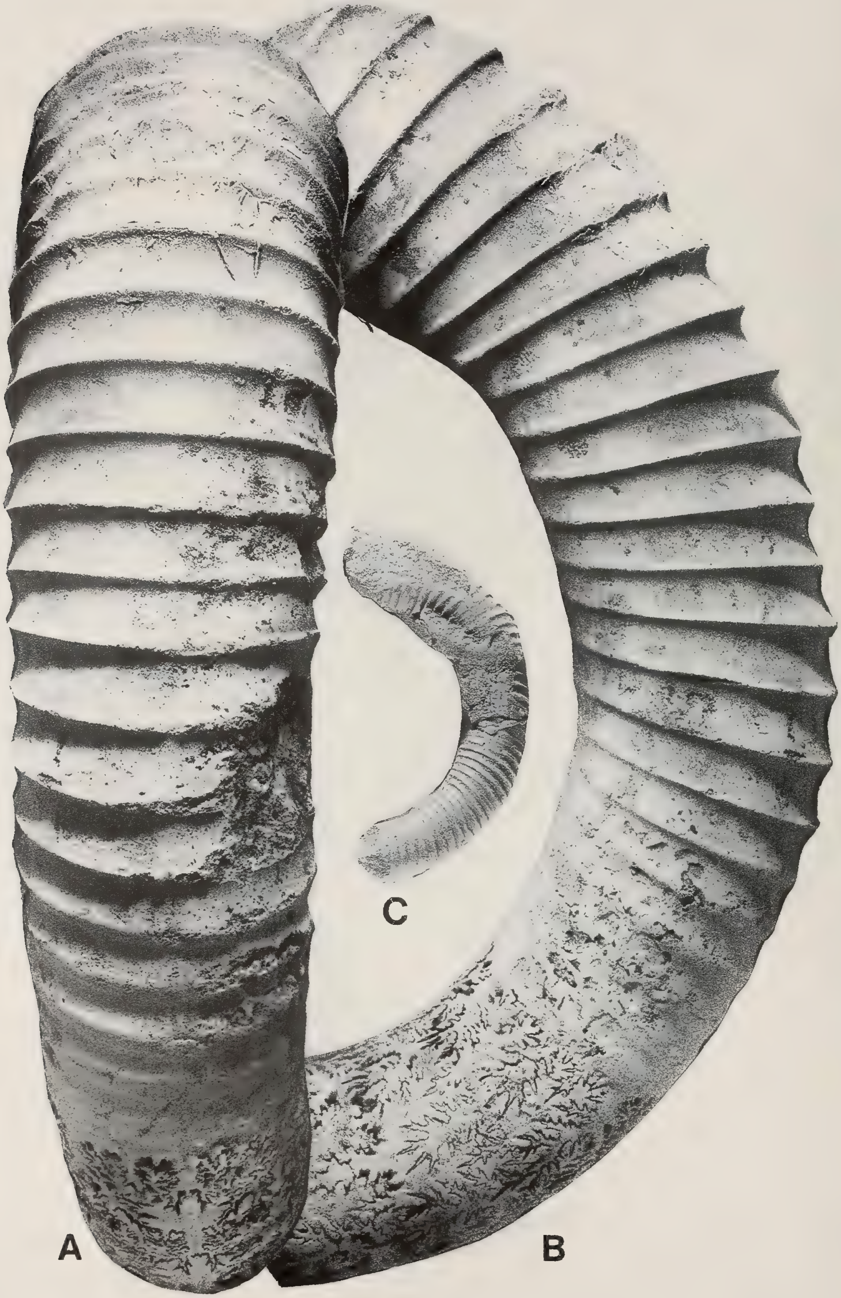

Figure 10

A–B. *Neoglyptoxoceras magnificum* Collignon, 1969. The holotype, GD12074 from Gisement 162 de la Coupe de Berere I (Belo sur Tsiribihina), lower Campanian, Zone of *Anapachydiscus wittekindi* & *Eulophoceras jacobi*, subzone of *Hourcquiella bererensis*, level of *Neogauthiericeras zafimahovai*. C. *Neoglyptoxoceras* sp. cf. *N. serta* Collignon 1969 *non* Müller & Wollemann, 1906 from locality 109C, KwaZulu, St Lucia Formation, Campanian III.

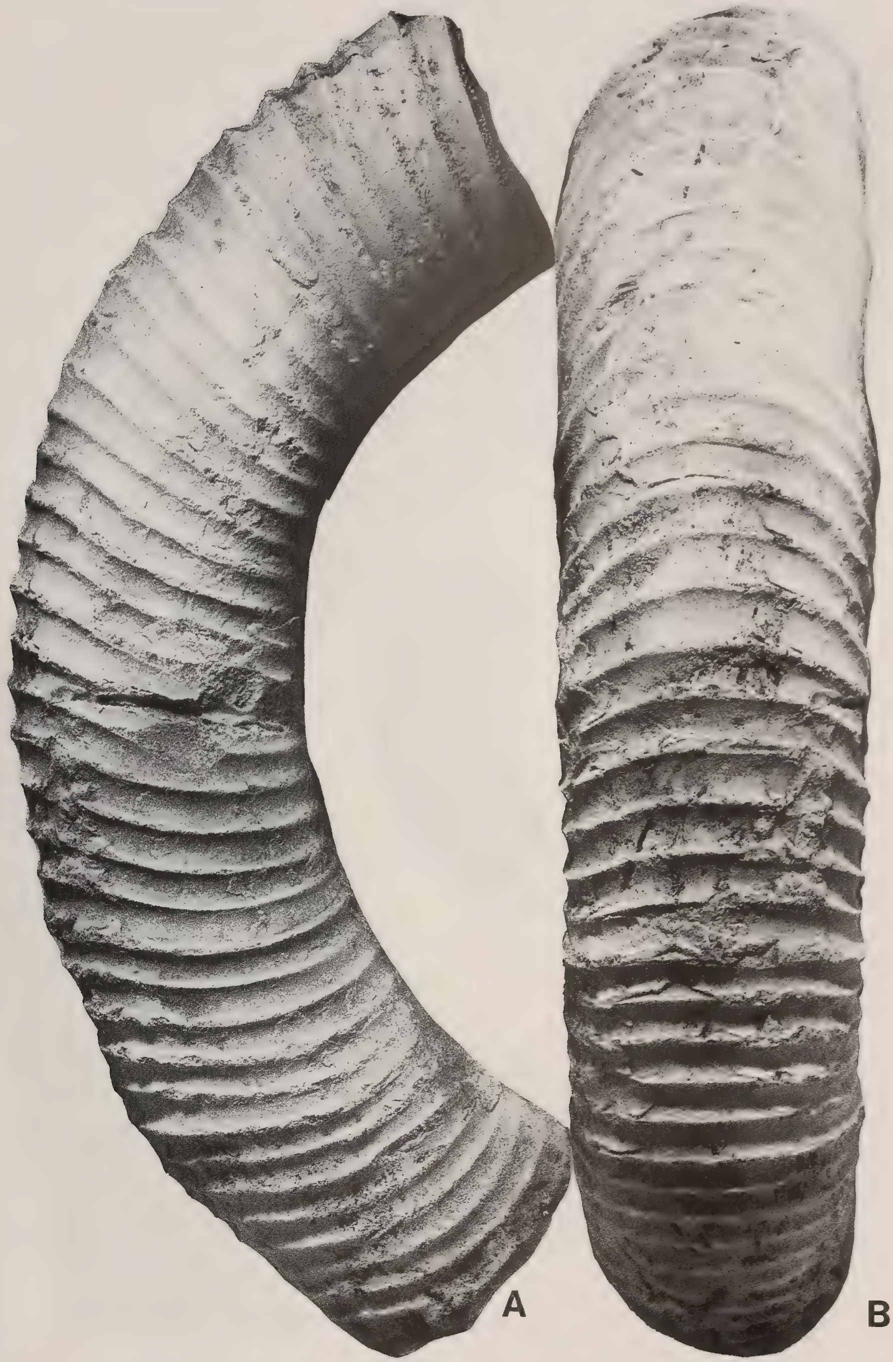

Figure 11

Neoglyptoxoceras perangustum Collignon, 1969. The holotype, GD12078 from Gisement 162, lower Campanian Zone of *Anapachydiscus wittekindi* & *Eulophoceras jacobi* subzone of *Hourcquiella bererensis*, Coupe de Berere I (Belo sur Tsiribihina). × 1.

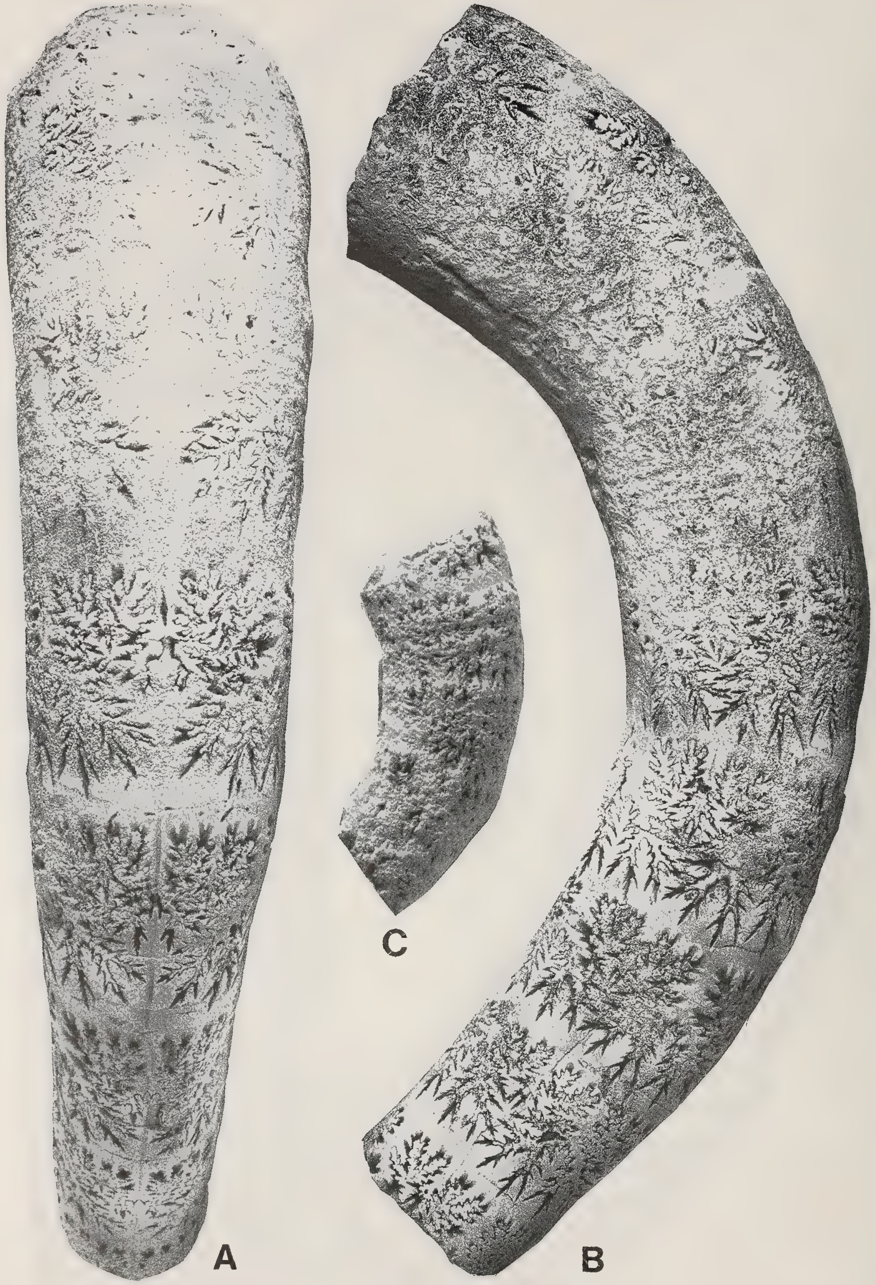

Figure 12

Neoglyptoxoceras annulatum (Collignon, 1969). A–B. GD12083, the holotype, from Gisement 312 du Km 16,200 de la Coupe Ampolypoly–Antsirasira–Behamotra (Belo sur Tsiribihina), lower Campanian, Zone of *Menabites boulei* & *Anapachydiscus arrialoorensis*. Note the smooth zone between successive sutures. C. Early whorls of *N. annulatum,* GD14013 from Gisement 162 de la Coupe de Berere I (Belo sur Tsiribihina), Zone of *Anapachydiscus wittekindi* & *Eulophoceras jacobi,* subzone of *Hourcquiella bererensis*. Level of *Neogauthiericeras zafimahovai*.

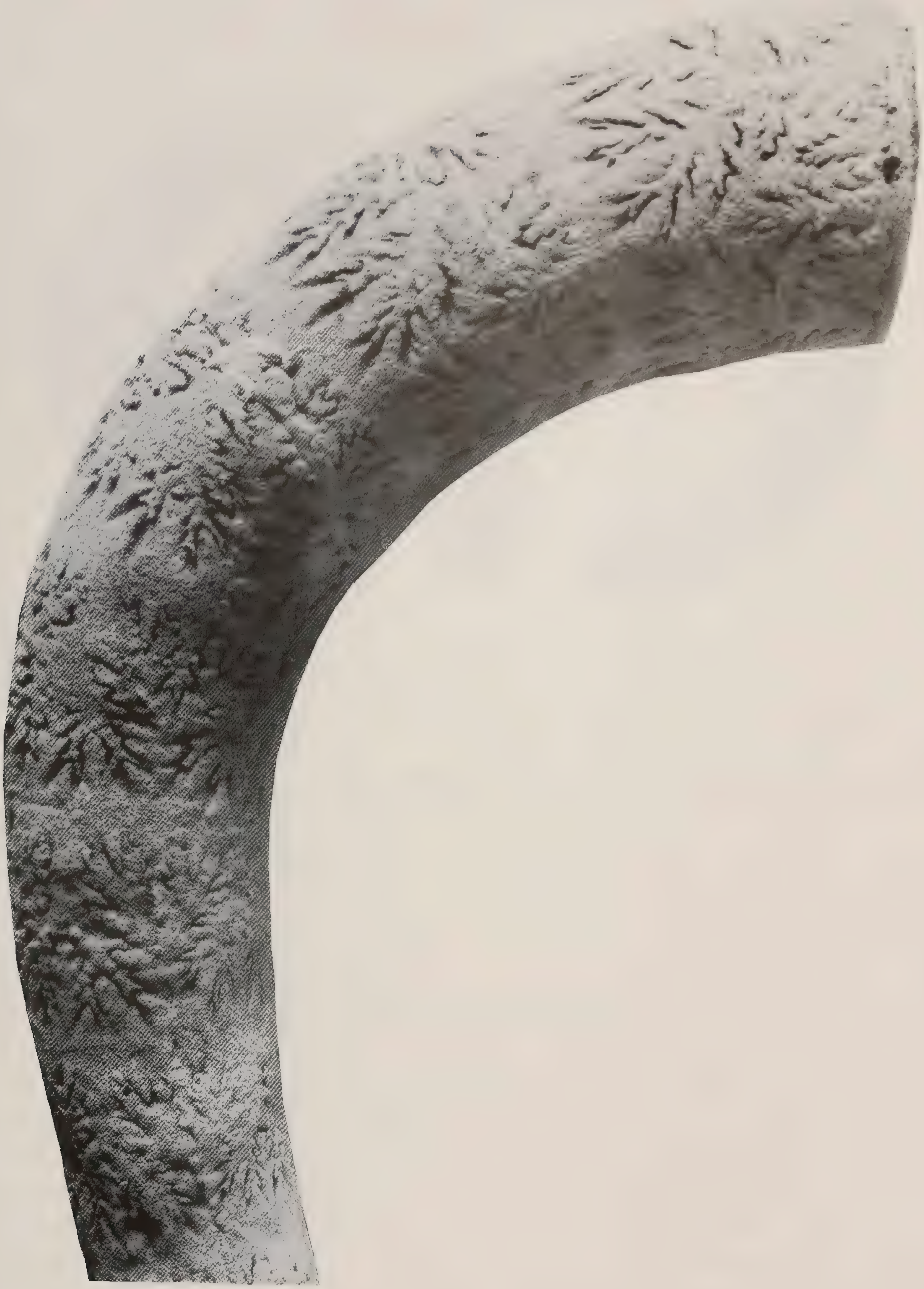

Figure 13

Neoglyptoxoceras annulatum (Collignon, 1969). GD14014 from Gisement 312 du Km. 16,200 de la Coupe Ampolypoly–Antsirasira–Behamotra (Belo sur Tsiribihina), lower Campanian, Zone of *Menabites boulei* & *Anapachydiscus arrialoorensis.* In the figure, the lower part of the shaft has been cropped to fit the page size. × 1.

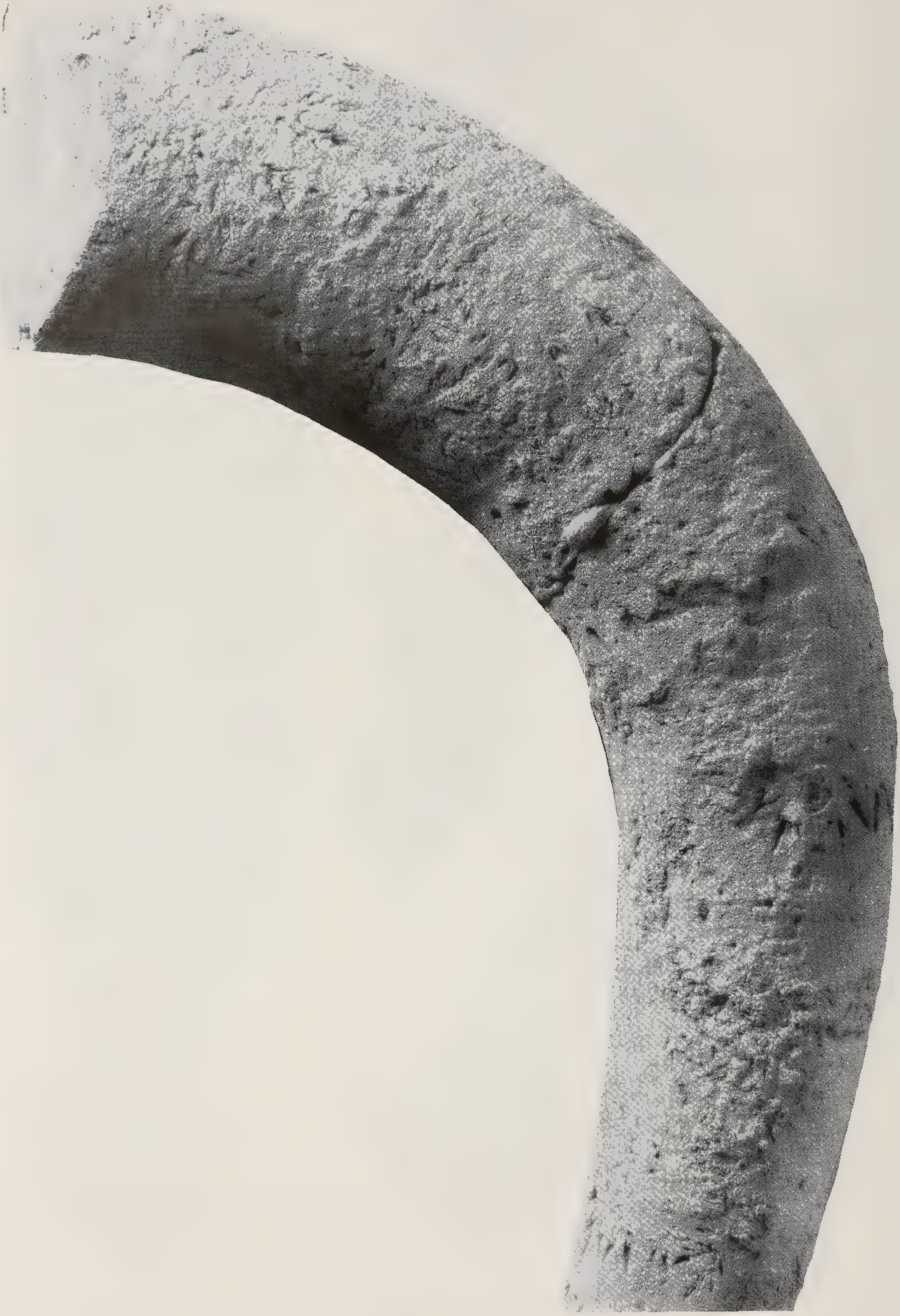

Figure 14

Neoglyptoxoceras annulatum (Collignon, 1969). The same specimen as figured in Fig. 10. In the figure, the lower part of the shaft has been cropped to fit the page size. × 1.

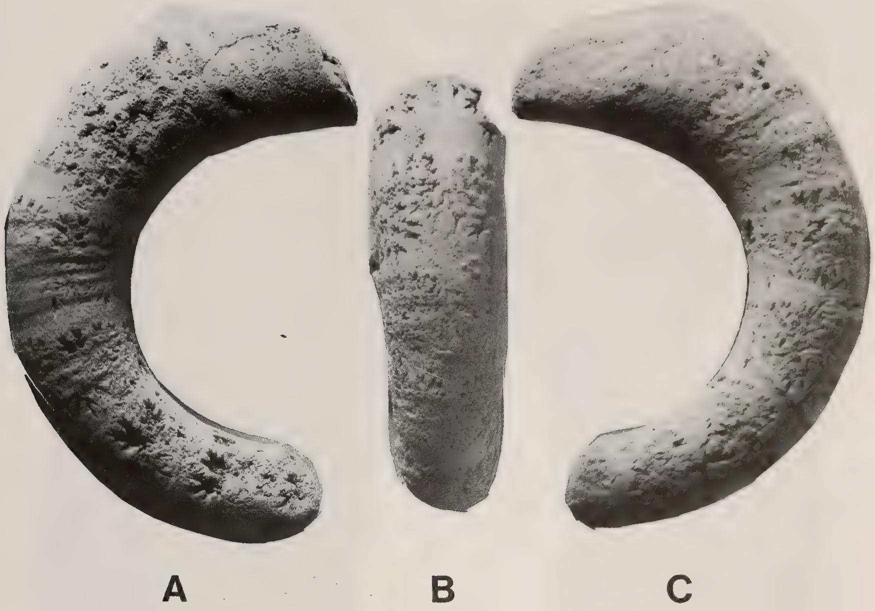

Figure 15

Neoglyptoxoceras annulatum (Collignon, 1969). GD14015 located imprecisely as Berere, lower Campanian. Early, criocone whorls. × 1.

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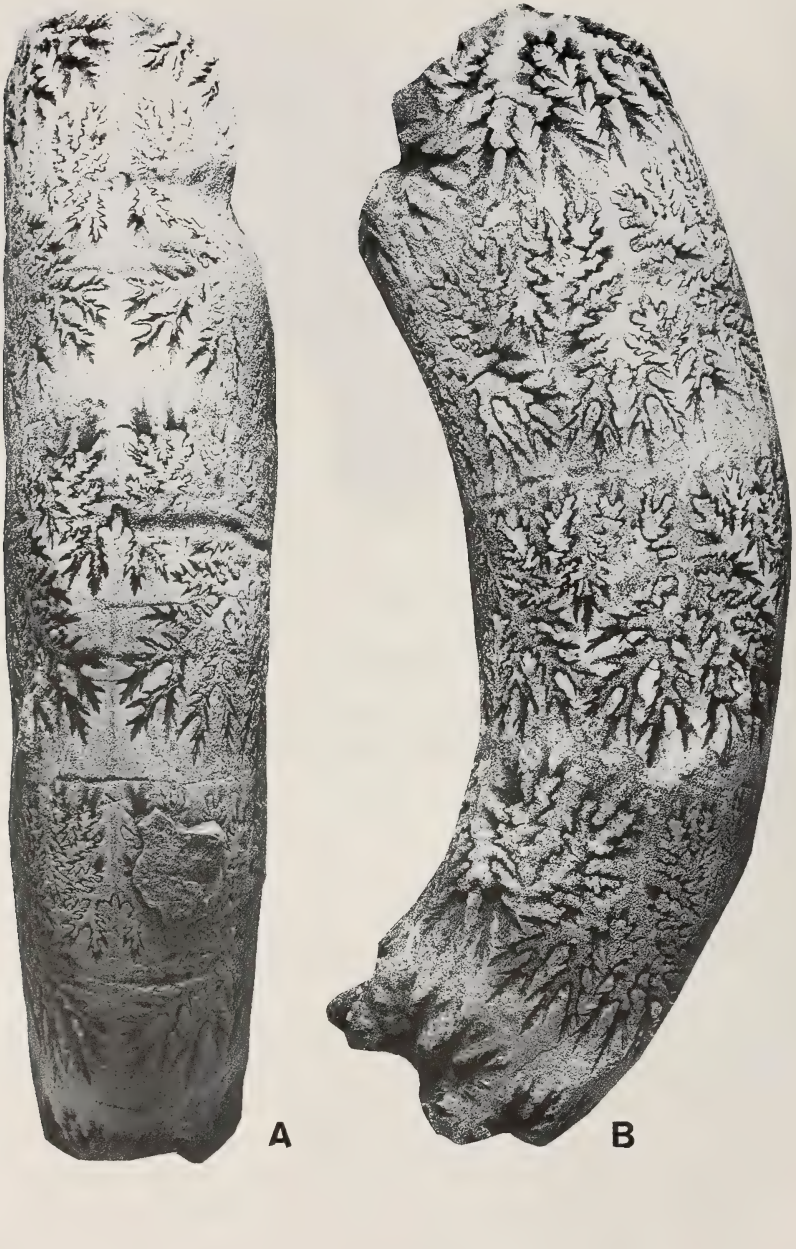

Figure 16

Neoglyptoxoceras giganteum (Collignon, 1969). GD12081, the holotype from Gisement 307 du Km. 15,500 de la coupe Ampolypoly–Antsirasira–Behamotra (Belo sur Tsiribihina), lower Campanian, Zone of *Menabites boulei* & *Anapachydiscus arrialoorensis*, subzone of *Rabeiella orthogonia.*

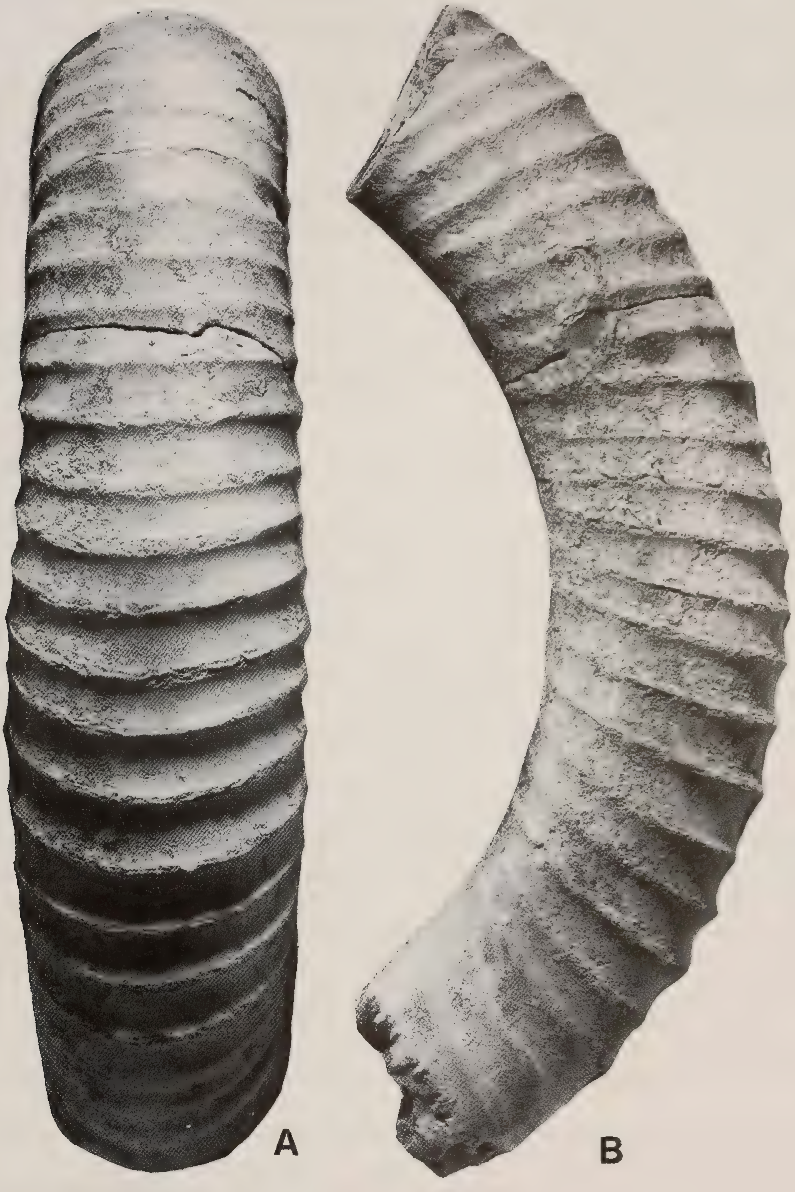

Figure 17

Neoglyptoxoceras magnificum Collignon, 1969. GD12075, part of the paratype figured by Collignon (1969: 35, pl. 526 (fig. 2075)) from Gisement 161, de Coupe de Berere I (Belo), Zone of *Anapachydiscus wittekindi* & *Eulophoceras jacobi*, subzone of *Hourcquiella bererensis*, level of *Neogauthiericeras zafimahovai*.

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OBSERVATIONS ON *PSEUDOXYBELOCERAS MATSUMOTOI* COLLIGNON, 1965 (CEPHALOPODA: AMMONOIDEA). ONTOGENY, SHELL STRUCTURE, DIFFERENTIAL PRESERVATION AND INTRASPECIFIC VARIATION

by

HERBERT CHRISTIAN KLINGER

&

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(With 10 figures)

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ABSTRACT

Examination of more than one hundred specimens of the Coniacian heteromorph ammonite *Pseudoxybeloceras matsumotoi* Collignon, 1965, from Madagascar and two from KwaZulu (Zululand) shows that coiling is in an open criocone and that, due to the shell structure, ornament varies considerably between internal moulds of the phragmocone and body chamber respectively, and in specimens with shelly preservation. The specimens also exhibit some variation in whorl section and ornamentation on both phragmocones and body chambers.

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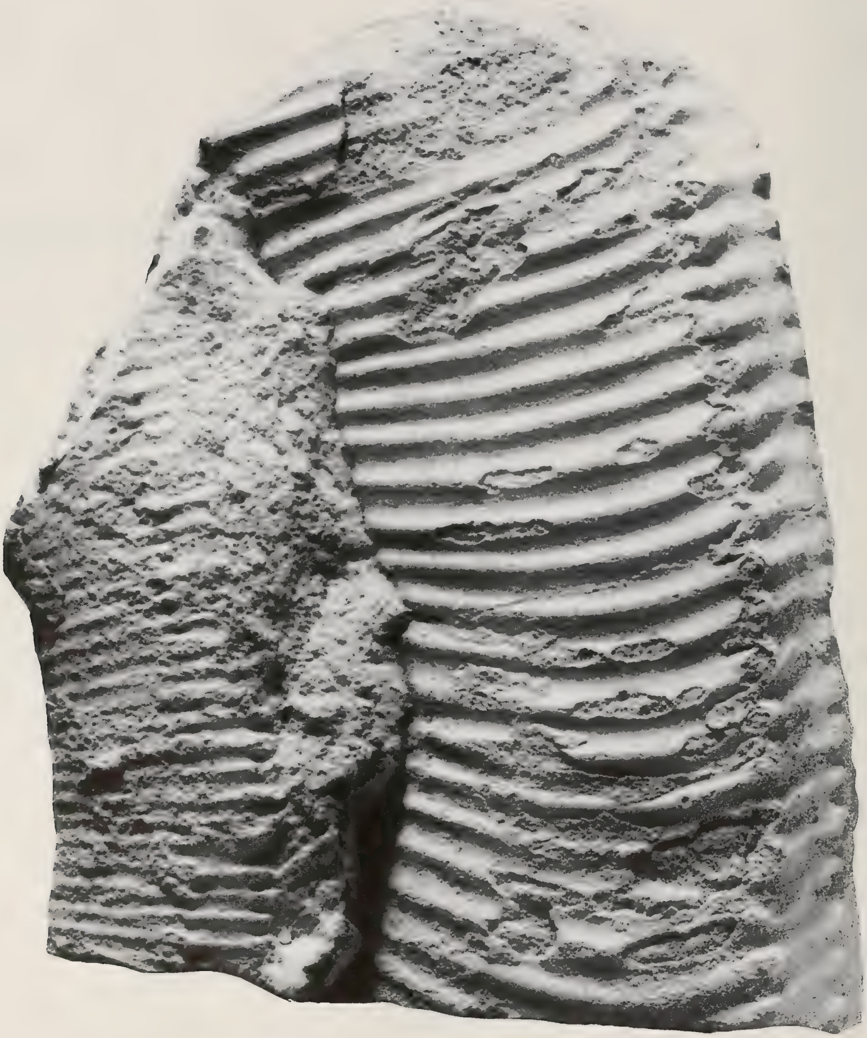

Figure 1

Pseudoxybeloceras matsumotoi Collignon, 1965. GD14000 from Gisement 462. The most complete specimen consisting of an inner phragmocone and an outer body chamber whorl, illustrating the apparent open, elliptical crioconic coiling of the adult shell. × 1.

INTRODUCTION

In 1999 and 1993 respectively we had the opportunity to examine both the type and undescribed material in the General M. Collignon collection of Cretaceous fossils from Madagascar, which is now permanently housed at the Centre des Sciences de la Terre, Université de Bourgogne, in Dijon. Amongst these, we were able to examine more than a hundred specimens of the Coniacian heteromorph ammonite *Pseudoxybeloceras matsumotoi* Collignon 1965 (1965: 12, pl. 419 (fig. 1731)). These, as well as two specimens from the Coniacian of Kwazulu, allow us to comment on the ontogeny, shell structure and resultant dissimilar appearance of ornamentation on the phragmocone and body chamber of internal moulds and, where shell is preserved, as well as on the intraspecific variation of the latter and of the whorl section.

MATERIAL

Madagascan material examined is from the localities ('Gisements') listed by Collignon (1965):

225. Ankotrofotsy (Antsalova). Coniacian sensu lato.

263. Masiaposa (Belo sur Tsiribihina). Lower Coniacian, Zone of *Peroniceras dravidicum.*

280. Coupe Ampolipoly–Antsitasira km 10,5 à 10,700 … qui pourrait être de la base du Campanien. (Note: this appears to be incorrect as all the other localities are Coniacian!)

335. Beantaly (Belo sur Tsiribihina). Middle Coniacian, Zone of *Kossmaticeras theobaldianum & Barroisiceras onilahyense.*

344. Analabe (Belo sur Tsiribihina). Middle Coniacian, Zone of *Kossmaticeras theobaldianum & Barroisiceras onilahyense.*

462. Manasoa (Betioky). Middle Coniacian, Zone of *Kossmaticeras theobaldianum & Barroisiceras onilahyense.*

467. Ravin d'Anjoho (Betioky). Middle Coniacian, Zone of *Kossmaticeras theobaldianum & Barroisiceras onilahyense.*

729. Ambiky, Sud Andimaka, pres Ampolipoly (Belo sur Tsiribihina). Middle Coniacian, Zone of *Kossmaticeras theobaldianum & Barroisiceras onilahyense.*

731. Coupe Andimaka-Iampolipoly. Middle Coniacian, Zone of *Kossmaticeras theobaldianum & Barroisiceras onilahyense.*

745. Coupe Ankinatsy–Souromaraina (Belo sur Tsiribihina). Middle Coniacian, Zone of *Kossmaticeras theobaldianum & Barroisiceras onilahyense.*

The two KwaZulu specimens, SAM–PCZ18747 and NMB–PCZ18743 respectively are from Kennedy & Klinger's (1975) localities:

Locality 92, Bed 1, Coniacian II, St Lucia Formation.

Locality 145, Coniacian II, St Lucia Formation.

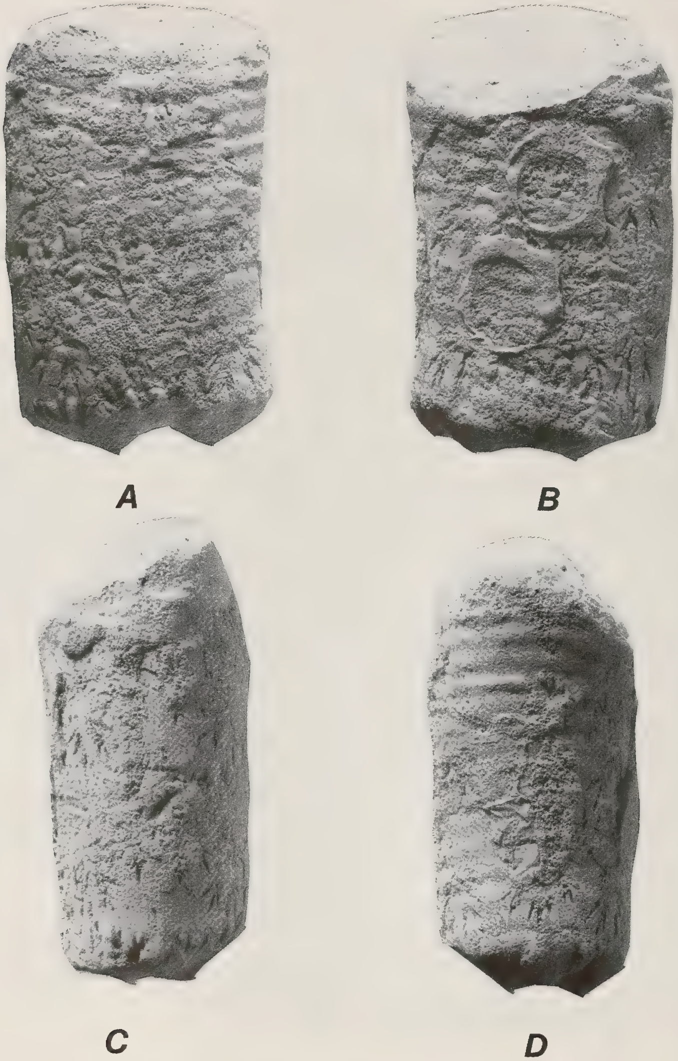

Figure 2

Pseudoxybeloceras matsumotoi Collignon, 1965. GD14001 from Gisement 225. An internal mould of the phragmocone to illustrate the weak ribbing on the flanks and dorsum, and absence over the venter as well as complete absence of tuberculation on internal moulds. × 1.

COILING

The initial juvenile stages are unknown; the earliest ontogenetic stages present consist of slightly curved shafts with a whorl height of *c*. 20 mm. With the exception of GD14000, all the specimens consist of slightly curved shafts only. GD14000 (Fig. 1) comprises parts of two slightly curved shafts situated next to each other and, though not in contact, probably belong to the same individual. The inner shaft is part of the phragmocone, the outer is body chamber. This suggests that coiling of the adult shell may have been in an open, elliptical criocone. An elliptical crioconic shell is also consistent with the taphonomy of the species. With no contact between the successive coils, the shell would have been extremely fragile and subject to post-mortem fragmentation. This would explain why nearly all of the material consists of parts of curved shafts only. Epizoan encrustation by serpulids and oysters of many of the specimens suggests an immediately post-mortem shallow depositional environment with currents strong enough to fragment most of the shells prior to burial.

When compared with later, Santonian-Campanian *Pseudoxybeloceras quadrinodosum* (Jimbo, 1894) (Wright & Matsumoto 1954, figs 9–12; Matsumoto 1977: 345, pl. 57 (fig. 2); pl. 6 (fig. 4); Szász 1974: 193, pl. 1 (figs 1–4); pl. 2 (figs 1–3)); pl. 3 (fig. 1); text-fig. 2; it appears that the trend in coiling in the genus *Pseudoxybeloceras* was from an open, elliptical criocone towards parallel, straight shafts linked by tightly curved sections, specifically in the body chamber which seems to have occupied two shafts. This seems to have been a common trend amongst genera conventionally referred to the Family Diplomoceratidae Spath, 1926 (Klinger & Kennedy this volume 110(4)).

SHELL STRUCTURE AND ORNAMENTATION

Details of the shell structure of ammonoids are reviewed by Kulicki (1996) and apart from a brief summary need not be repeated here. In all ammonoids, the post-embryonic shell consists of three principal layers:

1. The outer prismatic layer
2. The middle nacreous layer
3. The inner prismatic layer.

In most ammonoids, ornamentation of the outer part of the shell is the same as that of the inner part; the gross surface morphology of external and internal moulds is essentially similar. Also, the dorsal part of the ammonoid shell consists only of the inner prismatic layer. A well-documented exception to this rule amongst heteromorph ammonites occurs in the genus *Diplomoceras* Hyatt, 1900; specifically in the type and apparently only species definitely referable to the genus, *D. cylindraceum* (Defrance,1816) (see e.g. Olivero & Zinsmeister 1989: 627 with references and Klinger & Kennedy this volume 110(4)). Here, internal moulds of the phragmocone are generally perfectly smooth whereas specimens that retain the shell are distinctly ribbed. Furthermore, internal moulds of the body chamber in this species are always ribbed, thus suggesting a difference in shell structure between the phragmocone and body chamber. Ventral and dorsal parts of the

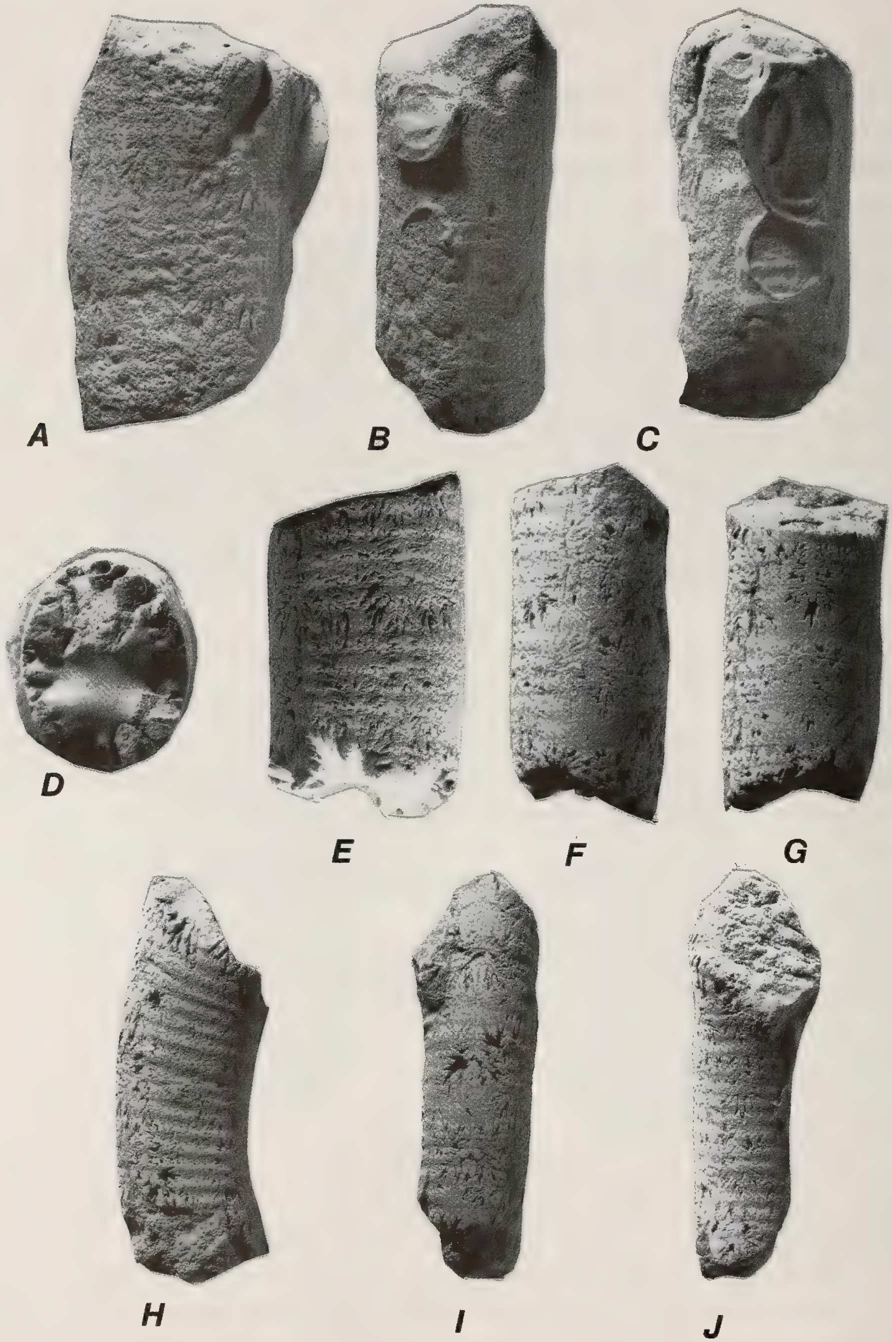

Figure 3

Pseudoxybeloceras matsumotoi Collignon, 1965. A–C. GD14002 from Gisement 225. D–G. GD14003. H–J. GD14004, both from Gisement 263. All internal moulds of the phragmocone to illustrate the weak ribbing on the flanks and over dorsum, and complete absence of tubercles. All × 1.

shell in *Diplomoceras* also appear to be the same, in contrast to "normally" coiled ammonites.

According to Olivero & Zinsmeister (1989) these apparent differences in ornament are due to the extreme thickening of the middle nacreous layer below the ribs on the phragmocone. Another notable feature of *Diplomoceras* is the discontinuous nature of the inner prismatic layer.

A similar situation occurs in *Pseudoxybeloceras matsumotoi*, although details differ, mainly because of the presence of tubercles on the ribs, in contrast to *Diplomoceras* which only has ribbing.

The majority of the specimens we have examined are internal moulds, both of the phragmocone and body chamber. Only two specimens, SAM–PCZ18747 and GD14009 retain parts of the original aragonitic shell, but in other specimens, parts of the original shell are preserved in recrystallized calcite.

Typical ornament in adult *Pseudoxybeloceras* as originally defined by Wright & Matsumoto (1954) consists of single ribs, each bearing a pair of ventral and ventrolateral tubercles, i.e. four tubercles per rib.

Internal moulds and sections of the body chamber that retain part of the original shell of *P. matsumotoi* show the typical quadrituberculate ribbing (e.g. Figs 1, 4E–G, 5–9). Details of the ornamentation on the different parts of the shell are to be discussed below.

In contrast, internal moulds of the phragmocone (e.g. Figs 2–3, 4A–D, 10C) vary from specimens that are virtually smooth, to specimens with faint ribbing on the flanks and over the dorsum, but absent on the venter, with no traces of tuberculation at all. Internal moulds such as these were referred to *Diplomoceras (Glyptoxoceras) subcompressum* (Forbes) by Collignon (1965: 13, pl. 419 (fig. 1732)) (Fig. 10C). The presence of ribbing on the flanks and over the dorsum, but their absence over the venter suggests that the inner prismatic layer is present in the former regions, and is either absent or very poorly developed over the venter. If this is the case, *P. matsumotoi* differs in this respect from *D. cylindraceum*, where the shell structure on the dorsum and the venter is the same according to Olivero & Zinsmeister (1989: 629).

As noted above, a few specimens retain either parts of the original aragonitic shell or recrystallized parts thereof. These show that construction of the greater part of the ornamentation, i.e. ribbing and tuberculation, is restricted to the middle, nacreous layer. The nacreous layer is thick, and forms solid, rather than hollow ribs and tubercles. Where the nacreous layer is well preserved, the ribs are prominent on the flanks and on the dorsum, but weaker-developed between the ventrolateral and ventral tubercles, and even weaker to absent between the latter over the venter. Both rows of tubercles in the nacreous layer are radially elongated with rounded upper surfaces and consist of solid shell. The solid nature of the ribs and tubercles is clearly indicated in specimens where these have been sheared off. In the case of the ventrolateral tubercles and ribs, these fractures are tear-shaped to narrowly elliptical (Figs 5A–B, 6, 8). In contrast, the ventral tubercles appear more rounded (Fig. 6A–C, 8), creating the impression that there was a basal septum to the original hollow tubercle. These fracture surfaces, however, are completely flat and irregular in outline, thus confirming the solid nature of the tubercles.

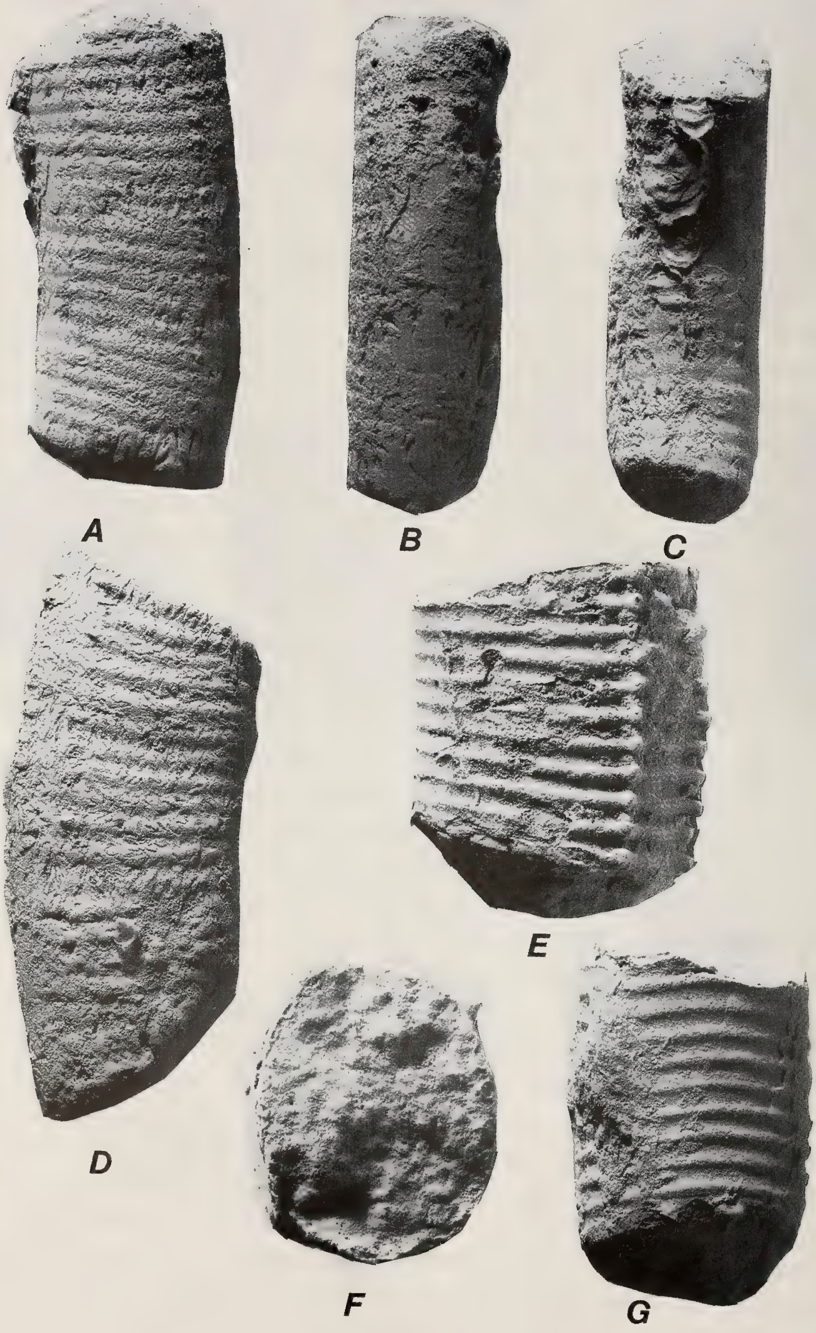

Figure 4

In SAM–PCZ18747 (Figs 7–8) parts of the complete shell are preserved over the ventral region. Here, an outer layer, which we suspect to be the prismatic layer, covers the tubercles of the nacreous layer and, in the case of the ventrolateral tubercles at least, forms delicate, hollow spines, each ending in a broad, flattened end (Figs 7A, 8). Without damaging the specimen for thin sectioning, it is impossible to determine whether this is indeed the outer prismatic layer, or part of the middle nacreous layer, but we suspect the former. It is not clear what, if any function, these spines performed. Hollow spines with a basal septum are common in diverse ammonite groups, especially in anisoceratid and turrilitid genera. Amongst the diplomoceratids, abnormal spines have been recorded in *Pseudoxybeloceras* aff. *lineatum* (Gabb) by Olivero (1988: 263, fig. 3) and in *Parasolenoceras soyaense* Matsumoto & Miyauchi 1986 (1986: 9, pl. 1 (figs 1–4); text-figs 1–2) and *Parasolenoceras tomitai* Matsumoto, 1984 (Matsumoto & Miyauchi 1986: 12, pl. 1 (fig. 5); text-figs 3–4).

INTRASPECIFIC VARIATION

Apart from the artefacts of differential preservation discussed above, and overall maximum size, there is little intraspecific variation in the material we have examined. A specimen with extremely coarse tuberculation is shown in Fig. 9E. The specimen shown in Fig. 9A–D, in contrast, has more delicate tuberculation and, in addition, has a distinctly depressed whorl section (Fig. 9C). We suspect the latter feature may be due to diagenetic deformation.

The most complete specimen, GD14000 (Fig. 1) discussed above, differs from the rest of the specimens in being much larger. The whorl height of the body chamber of that specimen is nearly twice that of the other specimens examined. It is not possible to say whether this merely reflects an extreme range in maximum size in the adult stage, or whether it is indicative of dimorphism.

Fig 4. (*see facing page*). *Pseudoxybeloceras matsumotoi* Collignon, 1965. A–C. GD14005 from Gisement 225. An internal mould of the phragmocone to illustrate weak ribbing on flanks and dorsum, and complete absence of tubercles. D. GD14006 from Gisement 263. An internal mould of the phragmocone with weak traces of ventrolateral and ventral tubercles. E–G. GD14007 from Gisement 335. A body chamber fragment with recrystallized shell showing typical *P. matsumotoi* ornament of quadrituberculate ribbing. All × 1.

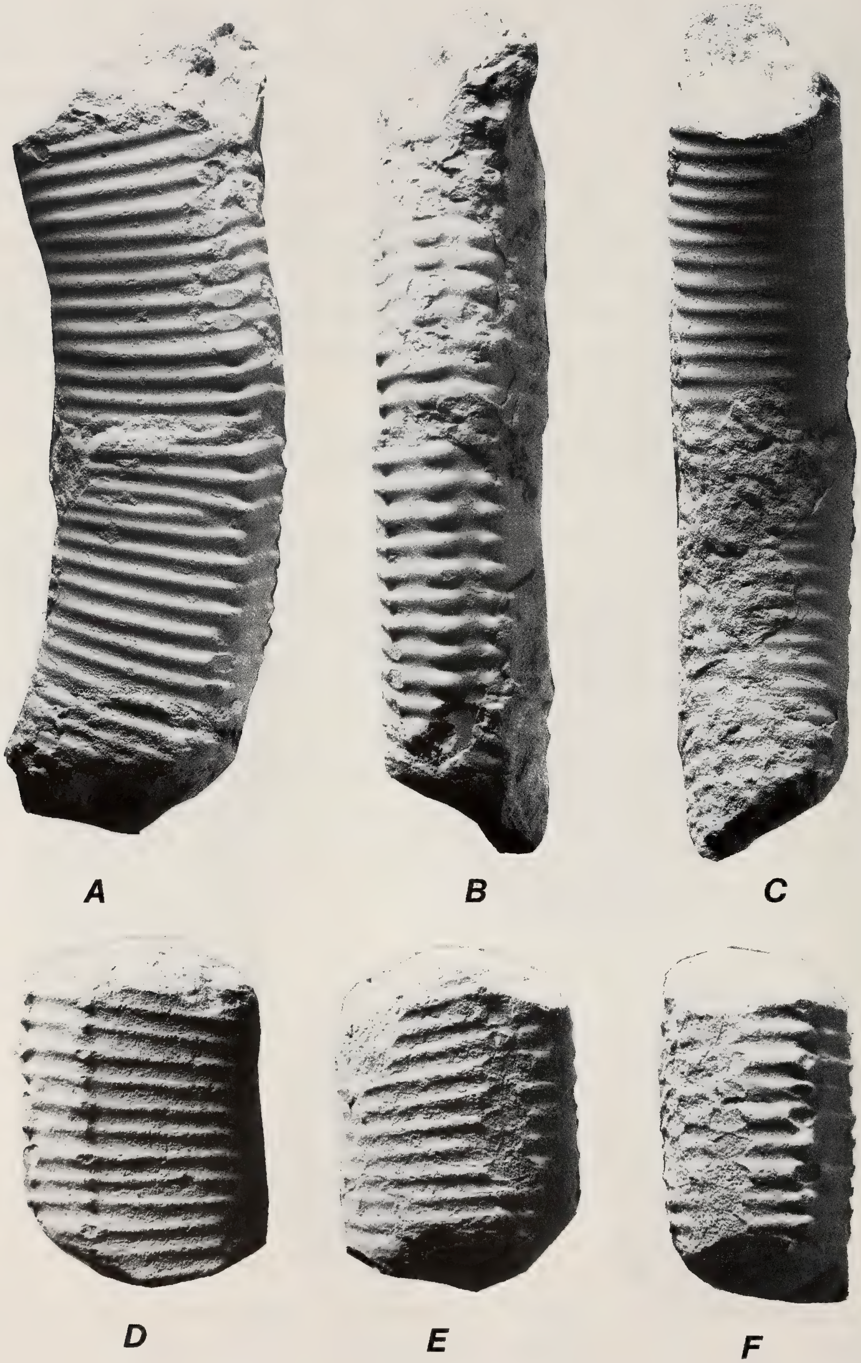

Figure 5

DIMENSIONS

The whorl height (Wh), whorl breadth (Wb) (in millimetres) and rib index (Ri) (ribs counted per whorl height) for figured specimens are as follows:

Specimen	Wb	Wh	Wb:Wh	Ri
GD14000	46,0	65,0	0,71	12
	20,0	28,0	0,71	11
GD14001	24,0	32,0	0,75	12
GD14002	22,0	28,0	0,79	–
GD14003	20,0	25,0	0,80	?10
GD14004	14,5	18,0	0,81	10
GD14006	22,0	29,0	0,76	10
GD14007	28,0	36,0	0,78	10
PCZ18743	22,0	29,5	0,75	9
GD14008	22,5	29,0	0,76	10
GD14009	25,0	34,5	0,72	9
GD14010	40,0	33,0	1,21	10

Fig 5. (*see facing page*). *Pseudoxybeloceras matsumotoi* Collignon, 1965. A–C. NMB–PCZ18743 from locality 145, KwaZulu. A body chamber fragment with most of the middle nacreous layer intact. This specimen shows the typical rounded elliptical shape of the tubercles, as well as the flat fracture surface where these have been sheared off. D–F. GD14008 Part of the phragmocone with part of the shell preserved in recrystallized calcite. Note the absence of tubercles on the internal mould (E, F) where the shell has not been preserved. Both × 1.

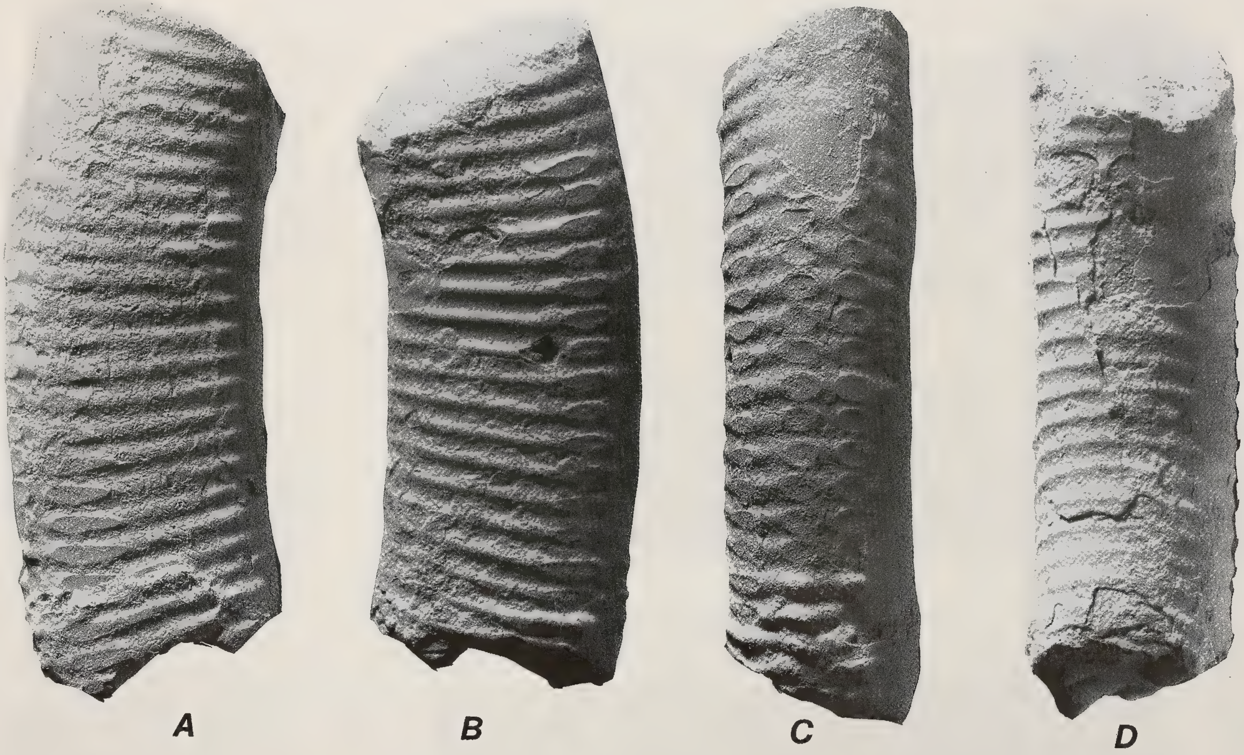

Figure 6

Pseudoxybeloceras matsumotoi Collignon, 1965. GD14009 from Gisement 731. A section of the phragmocone with part of the inner prismatic and middle nacreous layer preserved. Note the flat fracture surfaces on the flanks and on the venter where the solid ribs and tubercles have been sheared off. × 1.

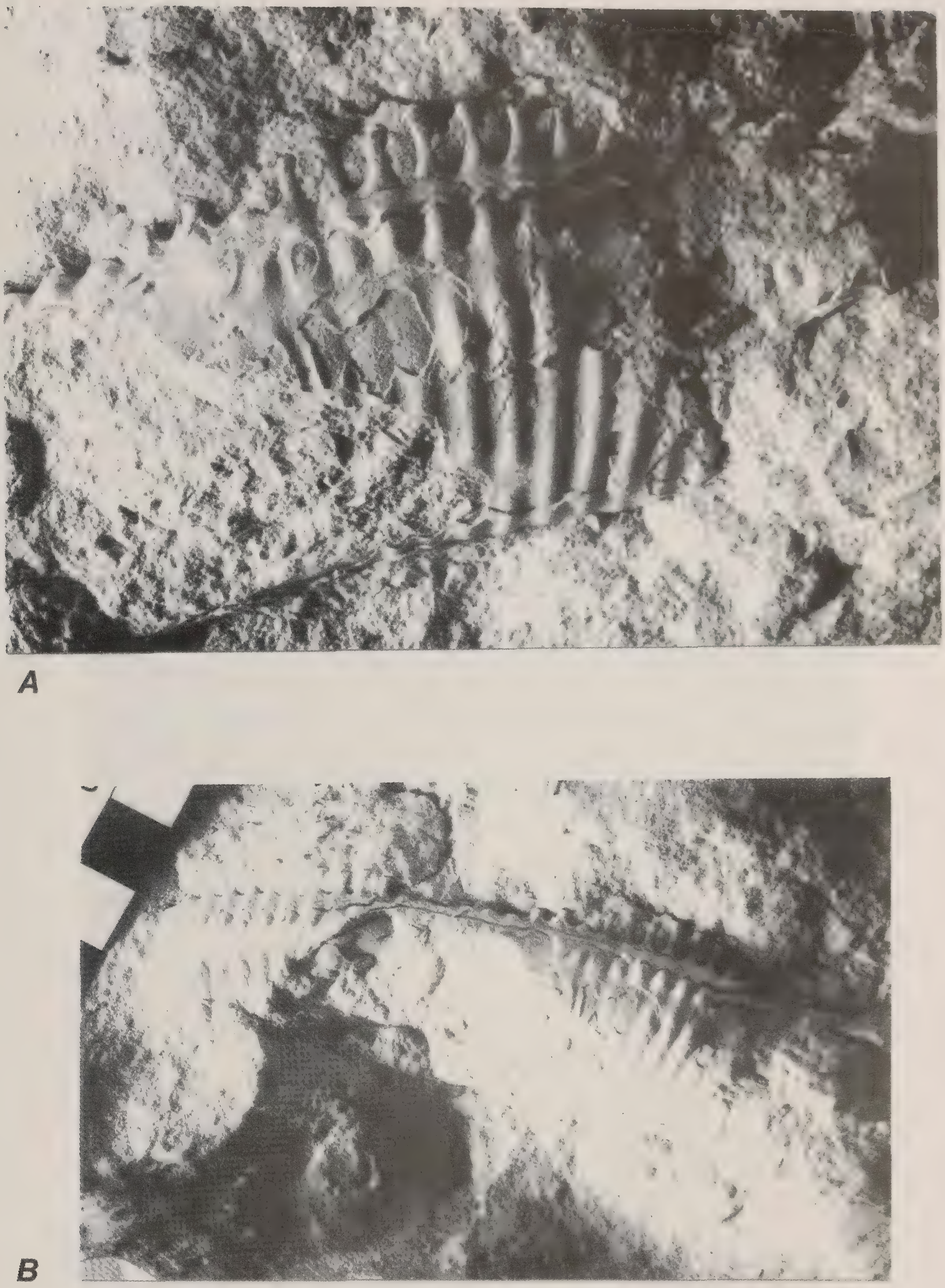

Figure 7

Pseudoxybeloceras matsumotoi Collignon, 1965. SAM–PCZ18747 from locality 92. A specimen which has part of the original aragonitic shell preserved. A. is an enlarged section of the septate section of B to show weak ribbing on the internal mould, radially elongated, rounded, solid ventrolateral tubercles of the middle nacreous layer, and the hollow ventral row of spines of what we suspect to be the outer, prismatic layer. A. × 2, B. × 1.

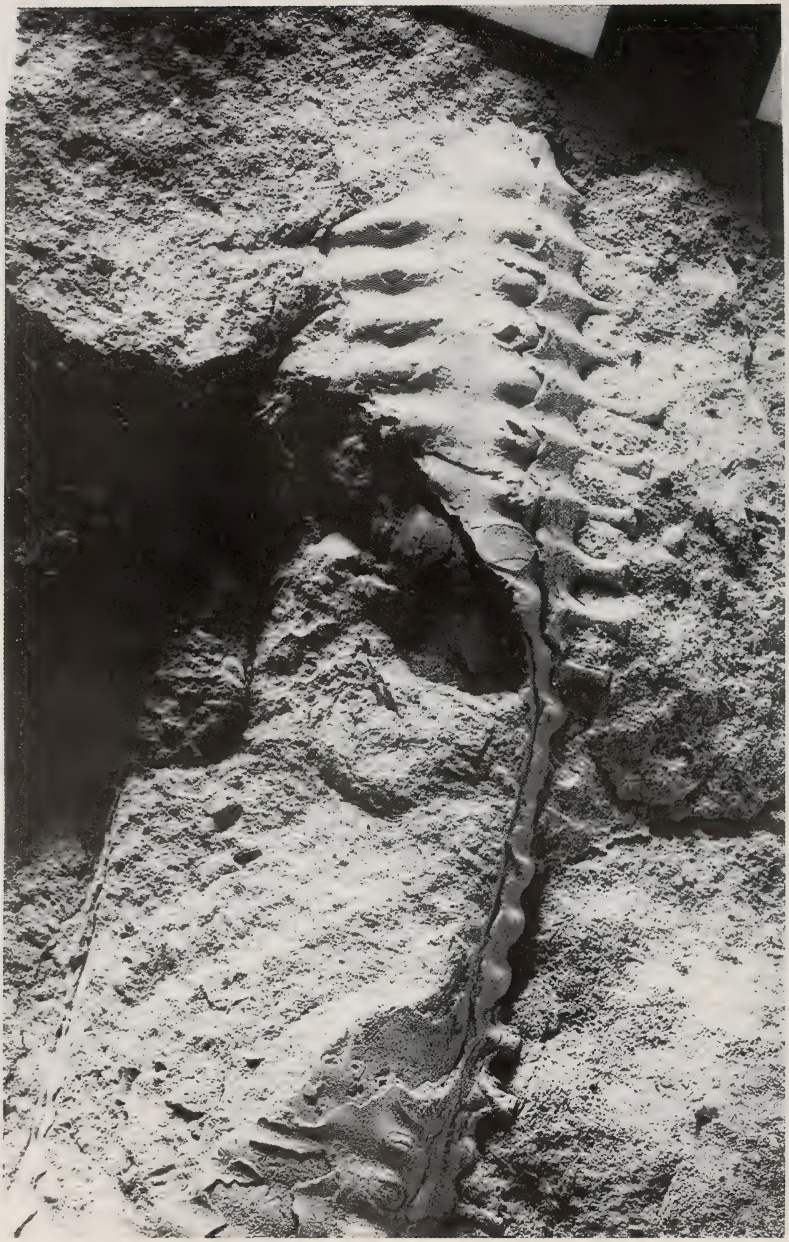

Figure 8

Pseudoxybeloceras matsumotoi Collignon, 1965. SAM–PCZ18747 from locality 92. Magnified section of the body chamber part of Fig. 7B to show details of ventral and ventrolateral tuberculation. × 2.

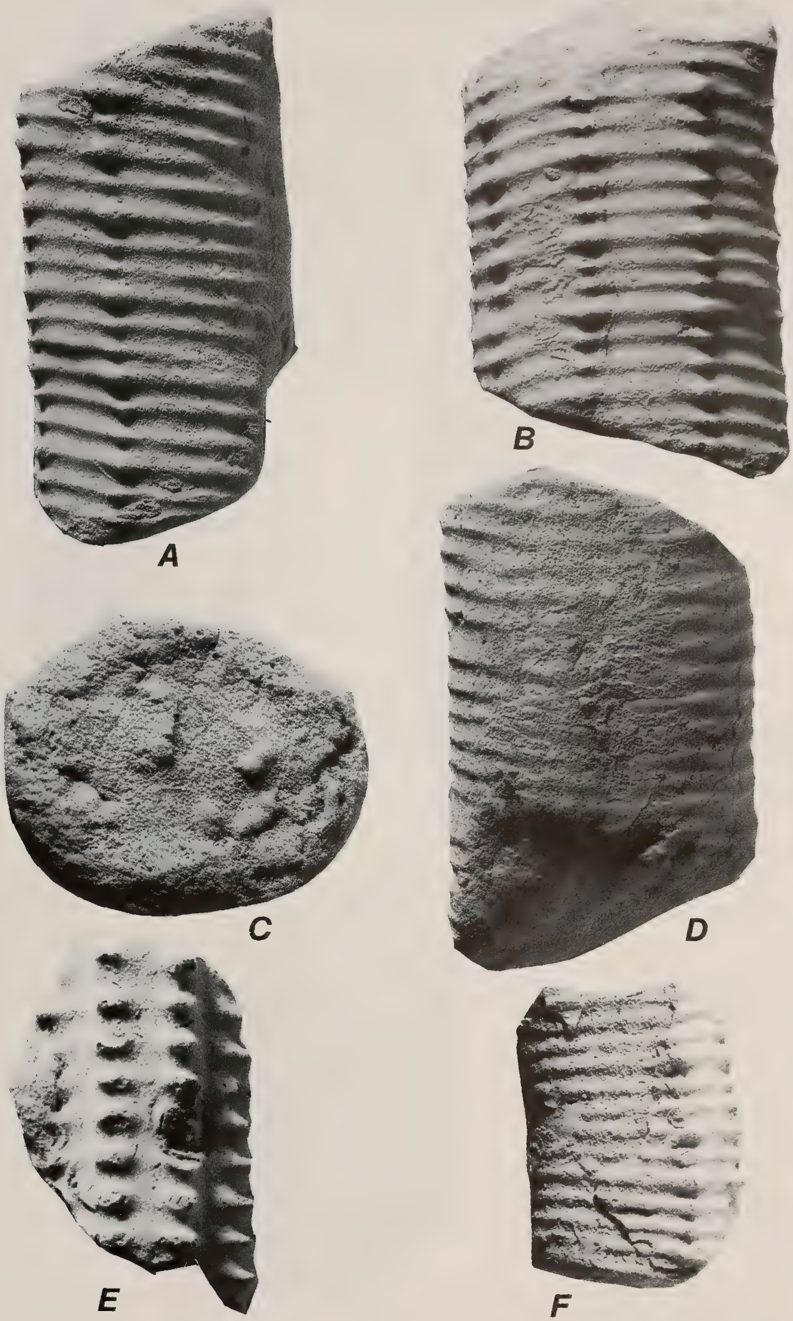

Figure 9

Pseudoxybeloceras matsumotoi Collignon, 1965. A–D. GD14010 from Gisement 280. E. GD14011 from Gisement 263. F. GD14012 from Gisement 335. Body chamber fragments to show variation in ornament and whorl section. E. shows extreme coarse tuberculation; A–D has a depressed whorl section which may be due to diagenetic deformation. All × 1.

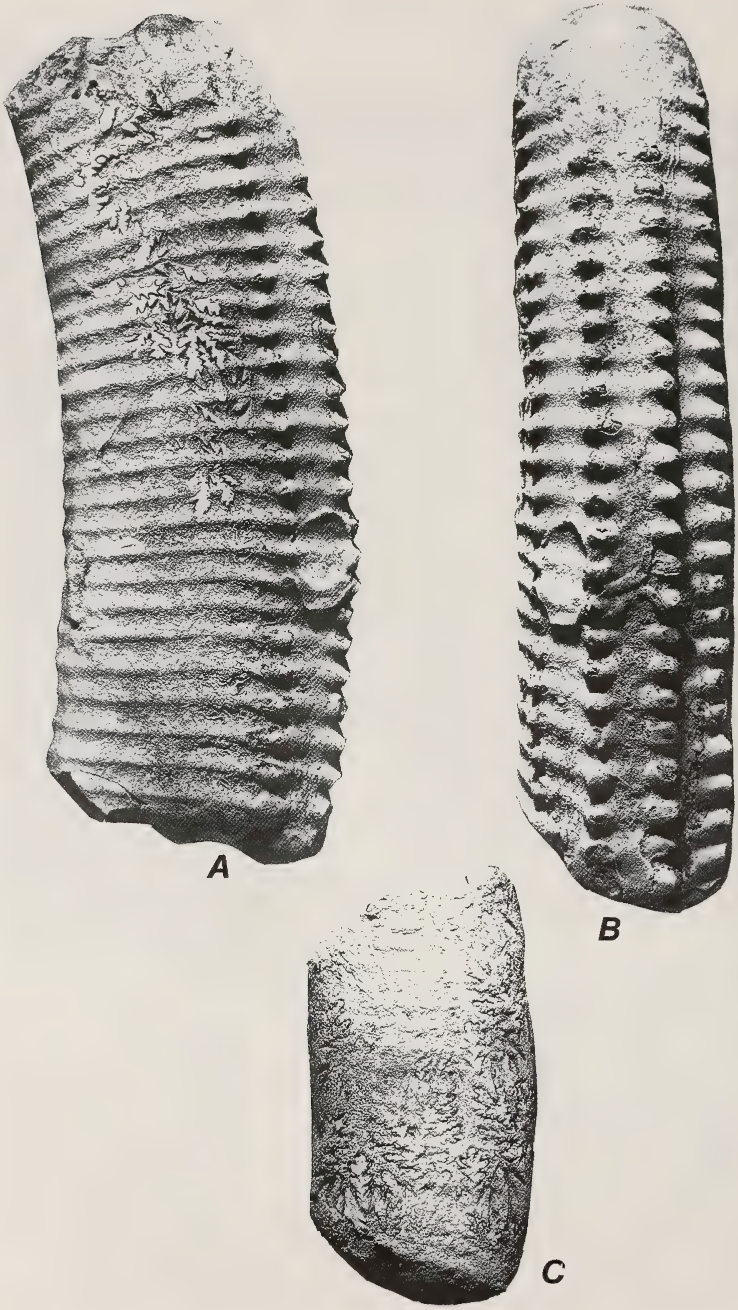

Figure 10

Pseudoxybeloceras matsumotoi Collignon, 1965. A–B. The lectotype here designated figured by Collignon (1965, pl. 419 (fig. 1731)) GD11731 from Gisement 335, Beantaly (Belo sur Tsiribihina), Lower or Middle Coniacian. C. "*Diplomoceras (Glyptoxoceras) subcompressum* Forbes" of Collignon 1965: 13, pl. 419 (fig. 1732), an internal mould of the phragmocone of *P. matsumotoi* from Gisement 225, Ankotrofotsy (Antsalova), Coniacian *sensu lato.* Both × 1.

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CRETACEOUS FAUNAS FROM ZULULAND AND NATAL, SOUTH AFRICA. THE AMMONITE FAMILIES NOSTOCERATIDAE HYATT, 1894 AND DIPLOMOCERATIDAE SPATH, 1926

by

HERBERT CHRISTIAN KLINGER

&

WILLIAM JAMES KENNEDY

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CRETACEOUS FAUNAS FROM ZULULAND AND NATAL, SOUTH AFRICA. THE AMMONITE FAMILIES NOSTOCERATIDAE HYATT, 1894 AND DIPLOMOCERATIDAE SPATH, 1926

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(With 64 figs)

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ABSTRACT

Some of the Upper Cretaceous heteromorph ammonites from Zululand and Pondoland, which had previously been described by Klinger (1976), are revised and refigured. New material and taxonomic data are incorporated in the present descriptions. The provisional classification adopted here is loosely based on that of Wright (1997) pending a full review of the relationships between the families Diplomoceratidae and Nostoceratidae. Representatives of the genera and subgenera *Eubostrychoceras (Eubostrychoceras)* Matsumoto, 1967, *E. (Amapondella)* Klinger & Kennedy, 1997, *Nostoceras (Nostoceras)* Hyatt, 1894, *Nostoceras (Bostrychoceras)* Hyatt, 1900, *Didymoceras (Didymoceras)* Hyatt, 1894, *Didymoceras (Eodidymoceras)* s. gen. nov., *Diplomoceras* Hyatt, 1900, *Glyptoxoceras* Spath, 1925, *Scalarites* Wright & Matsumoto, 1954, *Neoglyptoxoceras* Collignon, 1969, *Neocrioceras (Neocrioceras)* Spath, 1921*b*, *N. (Schlueterella)* Wiedmann, 1962, *Pseudoxybeloceras (Pseudoxybeloceras)* Wright & Matsumoto, 1954 and *Spiroxybeloceras* Kennedy & Cobban, 1999, are described, including the following new species: *Eubostrychoceras (Eubostrychoceras) nibelae* sp. nov., *E. (E.) zulu* sp. nov., *Didymoceras (Didymoceras) australis* sp. nov., *Didymoceras (Didymoceras?) africanum* sp. nov., *Didymoceras (Eodidymoceras) howarthi* sp. nov., *Neoglyptoxoceras collignoni* nom. nov., and *Neocrioceras (Neocrioceras) annelisae* sp. nov.

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INTRODUCTION

In 1976 Klinger described most of the known heteromorph ammonites from Zululand and Pondoland*, excluding the scaphitids and most of the baculitids. Unfortunately, during the editing process, reduced format working copies of the plates were substituted for the original plates. Consequently, the actual published figures were much smaller than the originals and of unsatisfactory quality. In this present contribution we refigure some of the 1976 material belonging to the families Nostoceratidae and Diplomoceratidae, as well as new material collected in the interim. Also, taxonomic changes and/or corrections are incorporated.

LOCATION OF SPECIMENS

The following abbreviations are used to indicate the location of specimens mentioned in the text.

GD	Centre des Sciences de la Terre, Université de Bourgogne, Dijon
NMB	National Museum, Bloemfontein
SAM	South African Museum
SAS	Council for Geosciences, Pretoria

FIELD LOCALITIES

Details of field localities are given by Kennedy & Klinger (1975); further descriptions of these localities are deposited in the Geological Collections, Oxford University Museum of Natural History, Department of Palaeontology, Natural History Museum, London and Division of Earth Sciences, South African Museum, Cape Town.

SUTURE TERMINOLOGY

The suture terminology of Wedekind (1916), reviewed by Kullmann & Wiedmann (1970) is followed here: I = internal lobe, U = umbilical lobe, L = lateral lobe, E = external lobe.

DIMENSIONS

Dimensions are given in millimetres. Wb = Whorl breadth; Wh = Whorl height; Wb:Wh = ratio of whorl breadth to whorl height. Prefixes Mx and Mn indicate maximum and minimum measurements. Ri = Rib index, ribs counted along the length of the specimen over a distance equal to the whorl height measured at the middle of that distance.

*In current geopolitical terminology, Zululand and Pondoland now form parts of the provinces of KwaZulu-Natal and Eastern Cape respectively. For the sake of continuity, we retain the names Zululand and Natal in the titles of our series of systematic descriptions of the ammonites from these regions.

CLASSIFICATION

Various attempts have been made to classify the genera referred to the families Nostoceratidae and Diplomoceratidae (amongst others Spath 1953; Wright 1957, 1997; Anderson 1958; Matsumoto 1959, 1967, 1977; Wiedmann 1962; Howarth 1965; Klinger 1976, 1982; Ward 1976; Ward & Mallory 1977; Cooper 1994). Broadly speaking, the genera were either lumped together or the families were split into numerous genera and subgenera, based on minute differences. None of these classifications corresponded and were neither satisfactory nor consistent. Reasons for this can be ascribed to many factors. Because of the loose coiling in most of the taxa, complete specimens are rare. The shells may be broken due to predation, taphonomic processes and during preparation from the matrix. Consequently, some genera were based on fragments and their diagnoses were incomprehensible. Furthermore, there is an extreme range of variation, not only within the same species, but in genera. In some, ornamentation was accorded priority, whereas in others the coiling was regarded as diagnostic. We are still not certain of the significance of the different coiling strategies of the early ontogenetic stages. To add to this, the Nostoceratidae and Diplomoceratidae show a rapid rate of evolution. Finally, dimorphism also has to be taken into consideration.

On completion of this largely descriptive section, we intend to publish a separate part on the classification and origins of the families Nostoceratidae and Diplomoceratidae, based on study of actual material at our disposal from various parts of the world. This is to be accompanied by an annotated list of species referred to the families, similar to that provided by the authors' description of the family Baculitidae Gill, 1871 (Klinger & Kennedy 2001).

For the purpose of description of the South African material below, we provisionally use a classification adapted from Wright (1997) with a few modifications.

SYSTEMATIC PALAEONTOLOGY

Suborder ANCYLOCERATINA Wiedmann, 1966
Superfamily TURRILITACEAE Gill, 1871
Family **Nostoceratidae** Hyatt, 1894
(= Jouaniceratidae Wright, 1952; Bostrychoceratinae Spath, 1953;
Hyphantoceratinae Spath, 1953; Emperoceratinae Spath, 1953;
Proavitoceratinae Spath, 1953 *errore pro* Pravitoceratinae)
Genus *Eubostrychoceras* Matsumoto, 1967

Type species

Eubostrychoceras indopacificum Matsumoto (1967: 333, pl. 18 (fig. 1)) by original designation of Matsumoto (1967: 332).

Diagnosis

Early ontogeny may be irregular, consisting of straight shaft(s) or heterostrophic whorls, followed by helically coiled stage that is either loosely or tightly coiled or a combination of both, and of variable duration, ending in a body chamber which may face upwards or embrace part or all of the helix. Ornament consists of simple ribs, in some with intercalated flared ribs at some stage or other. Tubercles generally absent.

Discussion

Two subgenera are here referred to *Eubostrychoceras*, *E. (Eubostrychoceras)* and *E. (Amapondella)* Klinger & Kennedy 1997. *Eubostrychoceras (Eubostrychoceras)* may have heterostrophic or hamitid to ptychoceratitid early whorls, followed by loosely or tightly coiled helical whorls. Ornament in most species consists of simple ribbing only; *E. (E.) japonicum* differs in having flared ribs in early and late ontogeny and incipient tuberculation. *Eubostrychoceras (E.) auriculatum* (Collignon, 1965) (Figs 3C, 7B–C) has flared ribs on the body chamber.

Eubostrychoceras (Amapondella) Klinger & Kennedy, 1997, differs from the nominal subgenus in having intercalated flared ribbing on part of the phragmocone and on the body chamber; the latter coils upwards and over the apex of the helical stage.

Subgenus *Eubostrychoceras* (*Eubostrychoceras*) Matsumoto, 1967

Type species

Eubostrychoceras (*Eubostrychoceras*) *indopacificum* Matsumoto (1967: 333, pl. 18 (fig. 1)), by original designation of Matsumoto (1967: 332).

Diagnosis

Early ontogeny consists of one or two, possibly three straight shafts; in rare cases heterostrophic, followed by helical whorls, either in close contact or loose, corkscrew-like. Aperture simple, facing obliquely upwards. Ornament in most species consists of simple ribbing and periodic constrictions. Suture moderately complex. Siphuncle situated at mid-flank.

Discussion

When Matsumoto (1967: 332) initially erected this (sub)genus, he included only forms with contiguous whorls, and with an upward-facing aperture that does not detach itself from the base of the spire. He also mentioned that the early whorls may show slightly irregular coiling and change in direction of ribbing. The type species, *E. (Eubostrychoceras) indopacificum* from the Coniacian of Japan, Madagascar and India (see e.g. Boule *et al.* 1907, pl. 7 (14) (fig. 1)) or Kennedy (1986, text-fig. 36)), shows the characters of the genus. Later, however, Matsumoto (1977: 324–329) expanded the scope of *Eubostrychoceras* s.s. to also include species with loosely coiled, helical whorls, as well as those with a detached, recurved body chamber. Essentially, *Eubostrychoceras* s.s. as interpreted subsequently by Matsumoto (1977) included virtually all the non-tuberculate species that had originally been referred to the genus *Bostrychoceras* Hyatt, 1900 except for the type species, *Bostrychoceras polyplocum* (Roemer, 1841).

Taxonomy within *Eubostrychoceras* s.s. is not easy. Wiedmann (1962: 202) included virtually the whole of what we regard here as *E. (Eubostrychoceras)* in a single 'super-species', *Cirroceras (C.) indicum*. This he divided into three subspecies based mainly on density of ribbing: *C. (C.) indicum saxonicum* (Schlüter, 1875) with 90 ribs per whorl, *C. (C.) indicum indicum* (Stoliczka, 1866) with 50 ribs per whorl and *C. (C.) indicum elongatum* (Whiteaves, 1903) with 25 ribs per whorl. This approach was initially adopted in describing the KwaZulu material by Klinger (1976), but in retrospect, we realize that Wiedmann's approach was unrealistic from both a taxonomic and stratigraphic point of view. Loosely and tightly coiled forms were included in the same subspecies and, even by heteromorph standards they had extremely long stratigraphic ranges—Turonian to Campanian.

We follow a more conservative interpretation of the subgenus. Based on coiling and ornamentation, two more or less distinct species groups can be recognized in the expanded subgenus *E. (Eubostrychoceras)*.

1. Group of *E. (Eubostrychoceras) indopacificum*. This includes nearly all the species originally included in *Eubostrychoceras* by Matsumoto (1967). Except for the very early whorls, discussed above, the greater part of the shell consists of a tightly coiled spire, ornamented by non-tuberculate ribs and constrictions only, ending in a slightly upwards facing aperture.
2. Group of *E. (Eubostrychoceras) otsukai* (Yabe, 1904) as interpreted by Collignon (1969). This group is easily identified by the generally loose, corkscrew-like coiling in the main part of the shell. The early whorls could be straight and in line with the axis of coiling, but not enclosed in the helix. The aperture also faces obliquely upwards.

Occurrence

Eubostrychoceras (Eubostrychoceras) first occurs in the lower Turonian, but only becomes common in the upper Turonian and persists through the Coniacian to the Campanian. The youngest possible *E. (Eubostrychoceras)* is a fragment recorded from the Maastrichtian of Nigeria by Reyment (1955: 15, pl. 1 (fig. 4)) as *Bostrychoceras* sp.

The genus is best known from the middle Turonian to the Campanian, with records from Japan, India, Madagascar, KwaZulu, North Africa, West Africa, Western Europe, the Pacific Coast of North America, and from the U.S. Western Interior.

Eubostrychoceras (Eubostrychoceras) indopacificum Matsumoto, 1967
Fig. 1D–G

1895 *Turrilites (Heteroceras) indicus* Kossmat (*non* Stoliczka), p. 143 [47], pl. 20 [6] (figs 5a–c, 6).

1907 *Turrilites (Bostrychoceras) polyplocus* Boule *et al.* (*non* Roemer), p. 61 [41], pl.14 [7] (figs 1–2).

1926 *Bostrychoceras indicum* Stoliczka; Tokunaga & Shimizu, p. 193, pl. 22 (fig. 4a–b), pl. 26 (figs 1–10).

1965 *Bostrychoceras indicum* Stol.; Collignon, p.10, pl. 418 (fig. 1726), p. 12, pl. 419 (figs 1727–1729).
?1965 *Bostrychoceras* sp. aff. *indicum* Stol.; Collignon, p. 12, pl. 419 (fig. 1730).
1967 *Eubostrychoceras indopacificum* Matsumoto, p. 333, pl. 18 (fig. 1).
1976 *Didymoceras (Didymoceras)* sp. gr. ex. *indicum* (Stoliczka); Klinger, p. 64 (*pars*), pl. 24 (fig. 3) only.
1986 *Nostoceras (Eubostrychoceras) indopacificum* Matsumoto; Kennedy, p. 101, text-fig. 36.

Type

Holotype is the specimen figured in Matsumoto (1967, pl. 18 (fig. 1)) from the Coniacian of Sakurazawa, Fukushima Prefecture, northwest Japan.

Material

SAM–PCZ18708 (ex SAS–Z1078), SAM–PCZ17332 (ex 33/li), both from locality 71, KwaZulu, St Lucia Formation, Coniacian I (?II).

Description

Both specimens are small and are probably microconchs. Coiling is dextral in SAM–PCZ18708 and sinistral in SAM–PCZ17332. The successive whorls are in close contact, but apparently not impressed into each other.

Ornament consists of predominantly single, slightly rursiradiate ribs—in SAM–PCZ18708 about 40 per whorl and in SAM–PCZ17332 about 70. Constrictions are common and conspicuous, occurring approximately once per half whorl. This results in all the constrictions being slightly offset, one above the other in a line parallel to the axis of coiling.

Discussion

Kaplan & Schmid (1988: 52) described the extent of variation in the upper Turonian to possibly basal Coniacian species *E. (E.) saxonicum*, and discussed the difficulty of separating it from allied species such as *E. (E.) indopacificum* and *E. (E.) muramotoi* Matsumoto, 1967. In terms of rib density, closely coiled Turonian–Coniacian species of *Eubostrychoceras* can be arranged from coarsely costate *E. (E.) matsumotoi* Cobban, 1987 with 20 to 30 ribs per whorl, through *E. (E.) indopacificum* with 50 to 55 per whorl, to *E. (E.) saxonicum* with 30 to 80 per whorl. In terms of rib density, our specimens clearly connect with *E. (E.) indopacificum* and *E. (E.) saxonicum*. The spacing of the constrictions is similar to that of *E. (E.) muramotoi* Matsumoto 1967. Our material is best referred to *E. (E.) indopacificum*.

Occurrence

Coniacian of Japan, India, Madagascar, and KwaZulu.

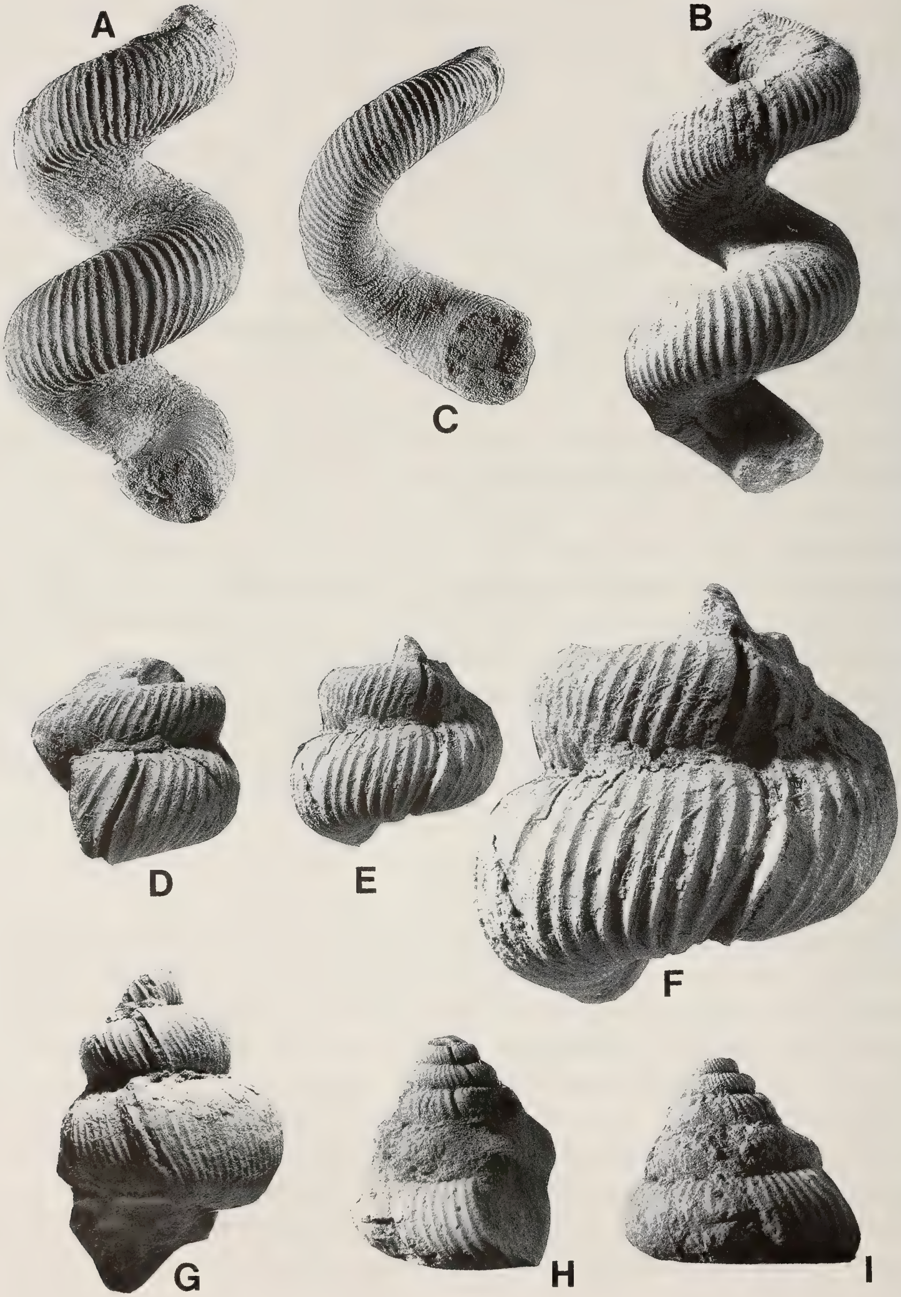

Figure 1

Eubostrychoceras (Eubostrychoceras) nibelae sp. nov.
Fig. 1H–I

1976 *Didymoceras (Didymoceras)* sp. gr. ex. *indicum* (Stoliczka); Klinger, p. 64 (*pars*), pl. 24 (fig. 4) only.

Type

Holotype by monotypy is SAM–PCZ17333 (ex A430) from locality 111, KwaZulu, St Lucia Formation, Campanian III.

Etymology

Named after the Nibela Peninsula on the northern side of Hell's Gates, which connect Lake St Lucia and False Bay, KwaZulu.

Description

Coiling is tight with a distinct zone of impression on the upper surface of the whorls. The apical angle (i.e. angle of the helically coiled part of the shell) is wide, approximately 65°. Ornament consists of about 60 slightly rursiradiate and sinuous ribs and regularly-spaced constrictions; one per whorl, resulting in their being aligned obliquely one above the other on the flanks.

Discussion

Even though we have only one specimen, the wide apical angle, tight coiling and regular spacing of the constrictions distinguishes this species from all other species of *E. (Eubostrychoceras)* in KwaZulu. The closest match in terms of ornament and constrictions is *E. (E.) indopacificum*, but that species has a smaller apical angle and is younger (Coniacian).

Occurrence

Campanian III of KwaZulu.

Fig 1. (*see facing page*). A–C. *Eubostrychoceras (E.) protractum* (Collignon, 1969). A–B. SAM–PCF17331 (ex Collignon Collection) from Gisement 719, km 10 000 de la coupe Ampamba Antsirasira (Belo sur Tsiribihina), Madagascar lower Campanian, Zone of *Menabites boulei* and *Anapachydiscus arrialoorensis*, subzone of *Termierella lenticulare*. C. SAM–PCZ18713 from locality 74, KwaZulu, St Lucia Formation, uppermost Santonian or lower Campanian. D–G. *Eubostrychoceras (E.) indopacificum* Matsumoto, 1967. D–F. SAM–PCZ18708. G. SAM–PCZ17332 (ex H33/li), both from locality 71, KwaZulu, St Lucia Formation, Coniacian III. H–I. *Eubostrychoceras (E.) nibelae* sp. nov., SAM–PCZ17333 (ex A430), the holotype from locality 110, KwaZulu, St Lucia Formation, Campanian II. A–E, H–I × 1; F × 2.

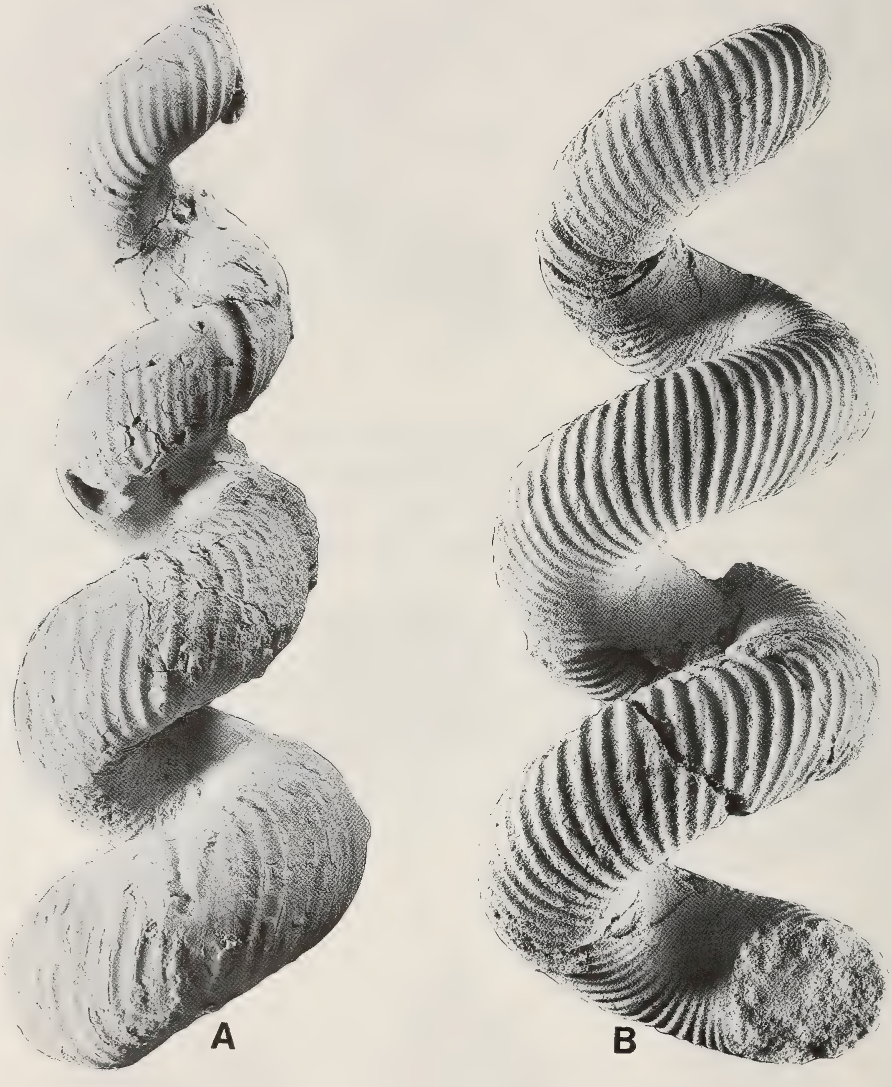

Figure 2

A. *Eubostrychoceras (E.) zulu* sp. nov. SAM–PCZ17334 (ex A432), the holotype, from locality 72, KwaZulu, St Lucia Formation, Coniacian II. B. *Eubostrychoceras (E.) otsukai* (Yabe, 1904). NMB–D1065, imprecisely located as 'Die Rooiwalle', but probably the same as locality 74, KwaZulu, St Lucia Formation, uppermost Santonian or basal Campanian. Both × 1.

Eubostrychoceras (Eubostrychoceras) zulu sp. nov.

Figs 2A, 63F

1976 *Didymoceras (Didymoceras)* sp. gr. ex. *indicum* (Stoliczka); Klinger, p. 64 (*pars*), pl. 24 (fig. 2) only.

Type

Holotype is SAM–PCZ17334 (ex A432) from locality 72, KwaZulu, St Lucia Formation, Coniacian II.

Etymology

Named after the geographic region of origin.

Material

Paratypes are SAM–PCZ18710 (ex A2278), SAM–PCZ18711 (ex A2272), SAM–PCZ18709 and SAM–PCZ18718, all from locality 72, KwaZulu, St Lucia Formation, Coniacian II.

Description

Coiling is in a loose helix with the distance between successive whorls about half the height of the previous whorl. The umbilical width increases with growth, but even at the largest preserved diameter, is still less than half the diameter of the whorls.

SAM–PCZ18709 (Fig. 63F) represents the earliest growth stage available, at a whorl diameter of 5 mm. Here, coiling is already distinctly helical, as in the later stages of growth. None of our specimens has the body chamber preserved, and we do not know if the helical mode of coiling continues right up to the aperture, or whether there is an upward change in direction as is characteristic of the subgenus.

Ornament consists of single, rounded ribs which are most prominent on the flanks and weakest on the dorsum. In the early stages of growth these are nearly radial, but with increasing diameter they become progressively rursiradiate and S-shaped. Prominent constrictions are already present on SAM–PCZ18709 at a whorl height of 6 mm, and occur on the whole phragmocone at a frequency of every 3/4 to 1 whorl.

The suture is complex. The position of the siphuncle is interesting. Instead of following the centre of the flanks, it follows a course nearly perpendicular to the axis of coiling.

Discussion

Eubostrychoceras (E.) zulu has coiling similar to that of *E. (E.) otsukai* (Yabe, 1904) and *E. (E.) protractum* (Collignon, 1969), but these are younger, Santonian-Campanian with larger umbilical widths and different ribbing.

Eubostrychoceras (E.) zulu superficially resembles *E. (E.) japonicum* (Yabe, 1904), which was comprehensively described and figured by Matsumoto (1977: 329, pl. 48 (figs 1–4), pl. 49 (figs 1–3), pl. 50 (figs 1–2), pl. 51 (figs 1–2), pl. 52 (fig. 3)). However, in *E. (E.) japonicum* the early whorls are heterostrophic and with a *Scalarites*-like ornament

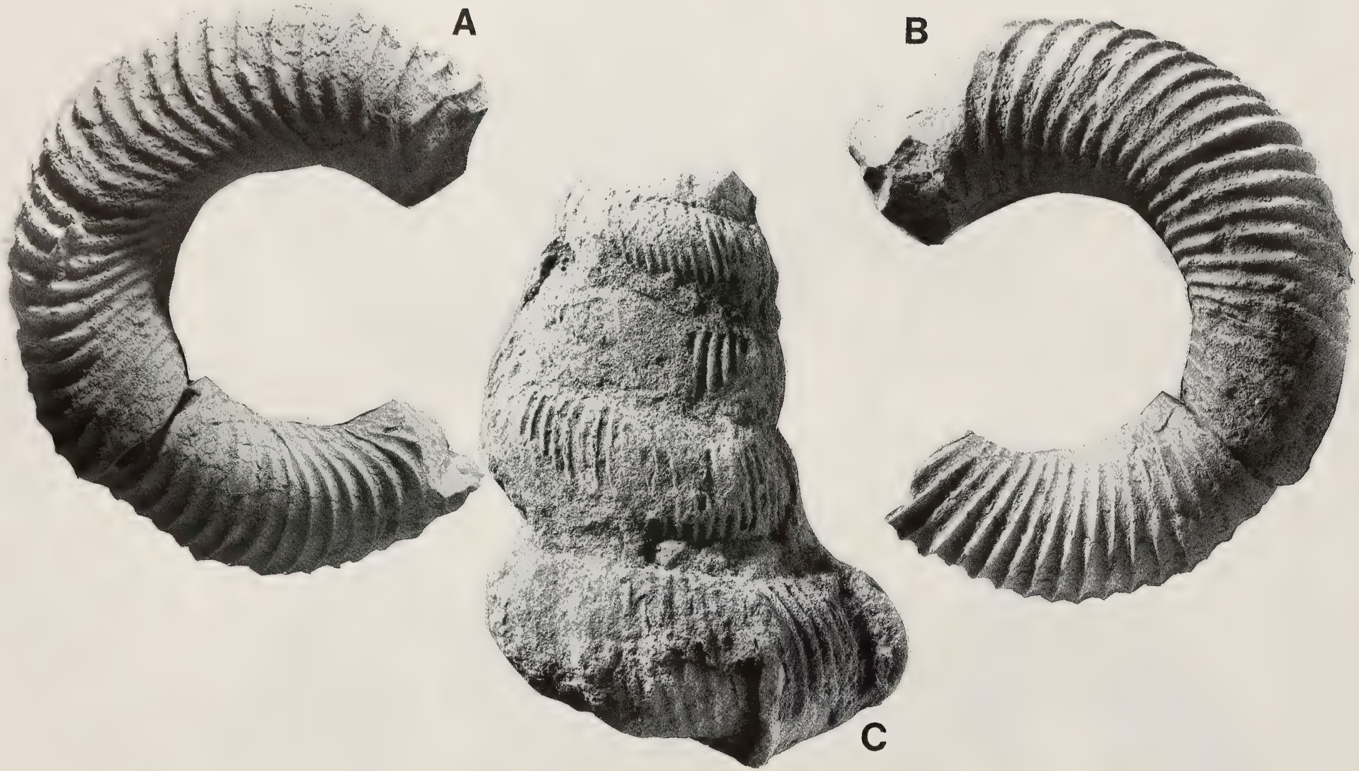

Figure 3

A–B. *Eubostrychoceras (E.) otsukai* (Yabe, 1904). SAM–PCZ17335 from locality 74, KwaZulu, St Lucia Formation, uppermost Santonian or basal Campanian. C. *Eubostrychoceras (E.) auriculatum* (Collignon, 1965). SAM–PCF17336 (ex Collignon Collection) from Beantaly, Madagascar, Coniacian. Both × 1.

(see Tanabe *et al.* (1981: 216, text-fig. 1; pl. 35 (fig. 1a–e)), Okamoto 1988, pl. 7 (fig. 9))—quite unlike those of *E. (E.) zulu*. Here, the earliest known whorls are already coiled in a corkscrew with uniform ribbing and constrictions. We suspect that the earliest part of the shell may have been straight as in *Hyphantoceras (H.) orientale* (Yabe) as figured by Okamoto (1988, pl. 7 (fig. 8)), pointing away from the helix.

Occurrence

Coniacian II of KwaZulu.

Eubostrychoceras (Eubostrychoceras) otsukai (Yabe, 1904)

Figs 2B, 3A–B, 4

1904 *Heteroceras* (?) *otsukai* Yabe, p. 14, pl. 4 (figs 1–2), pl. 6 (fig. 7).
1932 *Bostrychoceras Boulei* Collignon, p. 40, pl. 9 (fig. 4, 4a).
?1932 *Bostrychoceras Condamyi* Collignon, p. 39, pl. 9 (figs 1–2).
1969 *Bostrychoceras otsukai* (Yabe); Collignon, p. 31, pl. 524 (figs 2066–2068).
1969 *Bostrychoceras boulei* Coll.; Collignon, p. 34, pl. 525 (figs 2071–2072).

Type

Holotype is the specimen figured by Yabe (1904, pl. 4 (fig. 1)) from the Santonian of Kikumezawa, Ikushumbets, Hokkaido.

Material

NMB–D1065, imprecisely located as ‘northwestern end of False Bay’, but probably the same as locality 74, Die Rooiwalle, SAM–PCZ17335, SAM–PCZ9550 both from locality 74, KwaZulu, St Lucia Formation, uppermost Santonian or basal Campanian, SAM–PCZ18712 (ex H179/21) from locality 6, KwaZulu, uppermost Santonian or basal Campanian, SAM–PCZ12939 (ex H40/2) from field locality H40, Nyalazi, KwaZulu, St Lucia Formation, Campanian I.

Description

The most complete specimen NMB–D1065 (Fig. 2B) is preserved as an internal mould and consists of two and a half continuous whorls. The other specimens each consist of less than a whorl. In NMB–D1065 coiling is dextral in a loose helix with the distance between the successive whorls equal to about the height of the lower whorl. The umbilicus is very narrow and shows little if any increase in width from the early to the later whorls. The whorl section is virtually circular.

Ornament consists of about 36 to 50 slightly S-shaped, sharp-crested prominent ribs, separated by interspaces wider than the ribs themselves. SAM–PCZ18712 (Fig. 4) is the most coarsely ornamented with about 18 ribs per half whorl. On the adapical part of the whorl the ribs show a sudden ‘knick-point’ and, converging, continue in an apertural direction before passing radially, but much weakened over the dorsum. On the abapical part of the whorls the ribs do not show this sudden change in direction and merely weaken

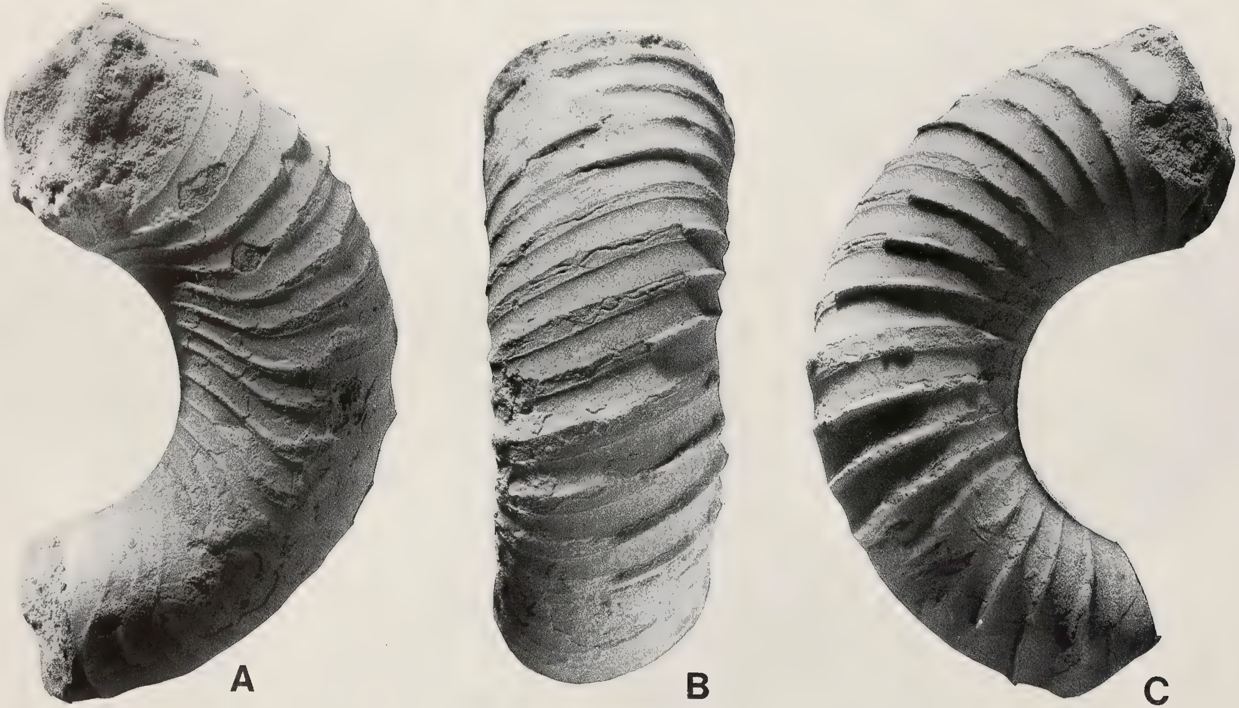

Figure 4

A–C. *Eubostrychoceras (E.) otsukai* (Yabe, 1904). SAM–PCZ18712 (ex H179/21) from locality 6, KwaZulu, St Lucia Formation, uppermost Santonian or basal Campanian. × 2.

towards the dorsum. Three prominent constrictions, approximately one per whorl, associated with an abapical flared rib are visible in NMB–D1065.

Discussion

The loose, corkscrew-like coiling and narrow umbilicus, associated with the distinctive ornament on the venter and adapical shoulder are characteristic of the species as interpreted by Collignon (1969: 31).

Matsumoto (1977: 331) stated that *Eubostrychoceras (E.) otsukai* is difficult to interpret on the basis of the type material, as well as separating it from the older (Turonian) *E. (E.) japonicum*. It is curious that Matsumoto did not discuss Collignon's (1969: 31) interpretation of *E. (E.) otsukai*. Should the Madagascan and KwaZulu material not belong to *E. (E.) otsukai*, we suggest that as first revising authors, the valid name for the material should be *E. (E.) condamyi* as originally described by Collignon (1932: 39, pl. 9 (figs 1–2)).

Eubostrychoceras (E.) japonicum has similar loose coiling on the major part of the phragmocone, but the ornament differs from that of *E. (E.) otsukai* as interpreted by Collignon (1969: 31). Ribbing continues virtually radially over the adapical edge instead of changing direction suddenly as in *E. otsukai*. Also, flared ribs occur on the early and late stages of ontogeny in *E. (E.) japonicum*. The Campanian specimen figured by Collignon (1932: 40, pl. 9 (fig. 3,3a)) as *Bostrychoceras japonicus* Yabe certainly does not belong to that species and is probably conspecific with *E. (E.) otsukai*.

Eubostrychoceras (E.) boulei Collignon (1932: 40, pl. 9 (fig. 4, 4a); 1969: 34, pl. 525 (figs 2071–2072)) is a similar loosely coiled species, but has a wider umbilicus, equal to twice the whorl width. We suspect that *E. (E.) boulei* is possibly only a looser coiled form of *E. (E.) otsukai*.

Eubostrychoceras (E.) protractum Collignon (1969: 31, pl. 524 (figs 2069–2070)) (see also below) is easily distinguished by the much finer and denser ribbing.

Occurrence

The type material of *E. (E.) otsukai* is dated as Santonian; the Madagascan specimens are abundant (Collignon 1969: 31 mentioned one hundred specimens) in the upper part of the lower Campanian. The KwaZulu material is probably also from the lower Campanian, but may extend down to the uppermost Santonian.

Eubostrychoceras (Eubostrychoceras) protractum Collignon, 1969
Fig. 1A–C

1969 *Bostrychoceras protractum* Collignon, p. 31, pl. 524 (figs 2069–2070).

Type

Holotype is the specimen figured by Collignon (1969, pl. 524 (fig. 2069)) from the lower Campanian of Gisement 320, Coupe Ampolypoly-Antsirasira-Behamotra (Belo sur Tsiribihina), Madagascar.

Material

SAM–PCZ18713, PCZ18714, PCZ18715, PCZ18716, PCZ18717, all imprecisely located as 'northwestern end of False Bay', probably the equivalent of our locality 74, Die Rooiwalle, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian.

Description

The ornament is very characteristic, consisting of fine, slightly rursiradiate ribs. These are strongest on the outer flank (venter) and weaken on the adapical and abapical umbilical shoulders. The ribs are typically single, but occasional irregular bifurcating or intercalatory ribs occur. The ribs number about 100 per whorl. Distinct constrictions are visible at all growth stages. In SAM–PCZ18717 two constrictions are present per half whorl.

Discussion

The loose coiling, dense ribbing and distinct constrictions are characteristic of the species. Our material is identical to that figured by Collignon, and topotype material (Fig. 1A–B).

As far as density of ribbing is concerned, the upper Santonian/lower Campanian loosely coiled *E. (Eubostrychoceras)* species can be arranged from coarsest *E. (E.) elongatum*, through *E. (E.) otsukai* to *E. (E.) protractum* (finest).

Eubostrychoceras (E.) densicostatum Matsumoto (1977: 332, pl. 52 (fig. 2)) has a comparable rib density, but the whorls are in contact in later stages of growth.

Occurrence

Lower Campanian of Madagascar, upper Santonian and/or lower Campanian of KwaZulu.

Eubostrychoceras (Eubostrychoceras?) sp.

Fig. 9D–E

Material

SAM–PCZ18750 from locality 105, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian.

Description and discussion

A single fragment from this locality differs from all other known heteromorphs from KwaZulu. It consists of part of a helical whorl which passes into a straight shaft with noticeable increase in whorl diameter, associated with a prominent constriction. Ornament consists of single, simple sharp ribs, separated by wide interspaces. No signs of tubercles are visible.

The small size and uncoiled body chamber clearly separates this specimen from all known species of *Eubostrychoceras* in KwaZulu. The absence of tubercles and the upper Santonian or lower Campanian occurrence of this specimen rule out the possibility that this might be a fragment of *Nostoceras*.

Occurrence

Upper Santonian or lower Campanian of KwaZulu.

Subgenus *Eubostrychoceras (Amapondella)* Klinger & Kennedy, 1997

Type species

Heteroceras amapondense Van Hoepen, 1921 (1921: 17, pl. 4 (figs 1–2)) by original designation of Klinger & Kennedy (1997: 246).

Diagnosis

Earliest whorls apparently helical, tightly coiled, followed by major part of shell which forms a low helix, and ending in an upcurved limb which reaches up to or slightly over the apex of the helical section. Ornament initially consists of simple ribbing only; at a later, variable stage, intercalated flared ribs occur.

Discussion

Klinger & Kennedy (1997: 244–246) recently discussed the affinities of the type species of *Eubostrychoceras (Amapondella)*, *Heteroceras amapondense* and concluded that it was neither a typical *Hyphantoceras* nor a *Madagascarites* as tentatively implied by Klinger's (1976: 71) reference to it as *Hyphantoceras (Madagascarites?) amapondense*.

Occurrence

Upper Santonian of Pondoland, offshore deposits of Natal Coast, KwaZulu, Israel, Austria, France and Mississippi, and lower Campanian of Madagascar and KwaZulu.

Eubostrychoceras (Amapondella) amapondense (Van Hoepen, 1921)

Figs 5, 6, 7A, 8A–D, 9A–C

1906 *Heteroceras* sp. Woods, p. 339, pl. 42 (fig. 4).
1906 *Heteroceras* sp. Woods, p. 339, pl. 42 (fig. 5).
1906 *Hamites (Anisoceras)* sp. Woods, p. 340, pl. 44 (fig. 3).
1921 *Heteroceras amapondense* Van Hoepen, p. 17, pl. 4 (figs 1–2).
1921*a* *Bostrychoceras*? sp. Spath, p. 255, pl. 24 (fig. 2).
1921*a* *Bostrychoceras*? sp. nov. Spath, p. 252.
1969 *Anaklinoceras stephensoni* Collignon, p. 50, pl. 532 (fig. 2096).
1969 *Hyphantoceras reussianum* d'Orb; Collignon, p. 38, pl. 527 (figs 2079–2080).
1976 *Hyphantoceras (Madagascarites?) amapondense* (Van Hoepen); Klinger, p. 71, pl. 32 (fig. 5a–b), pl. 33 (figs 2–3), text-fig. 10d–e.
1976 *Hyphantoceras (Hyphantoceras)* sp. A. Klinger, p. 70, pl. 32 (figs 2–4), pl. 32 (fig. 1).
1979 *Hyphantoceras (Madagascarites?) amapondense* (Van Hoepen); Summesberger, p. 123, pl. 3 (fig. 19), text-fig. 13.
1980 *Hyphantoceras (Madagascarites?) amapondense* (Van Hoepen); Summesberger, p. 277, pl. 1 (fig. 2), text-fig. 3.

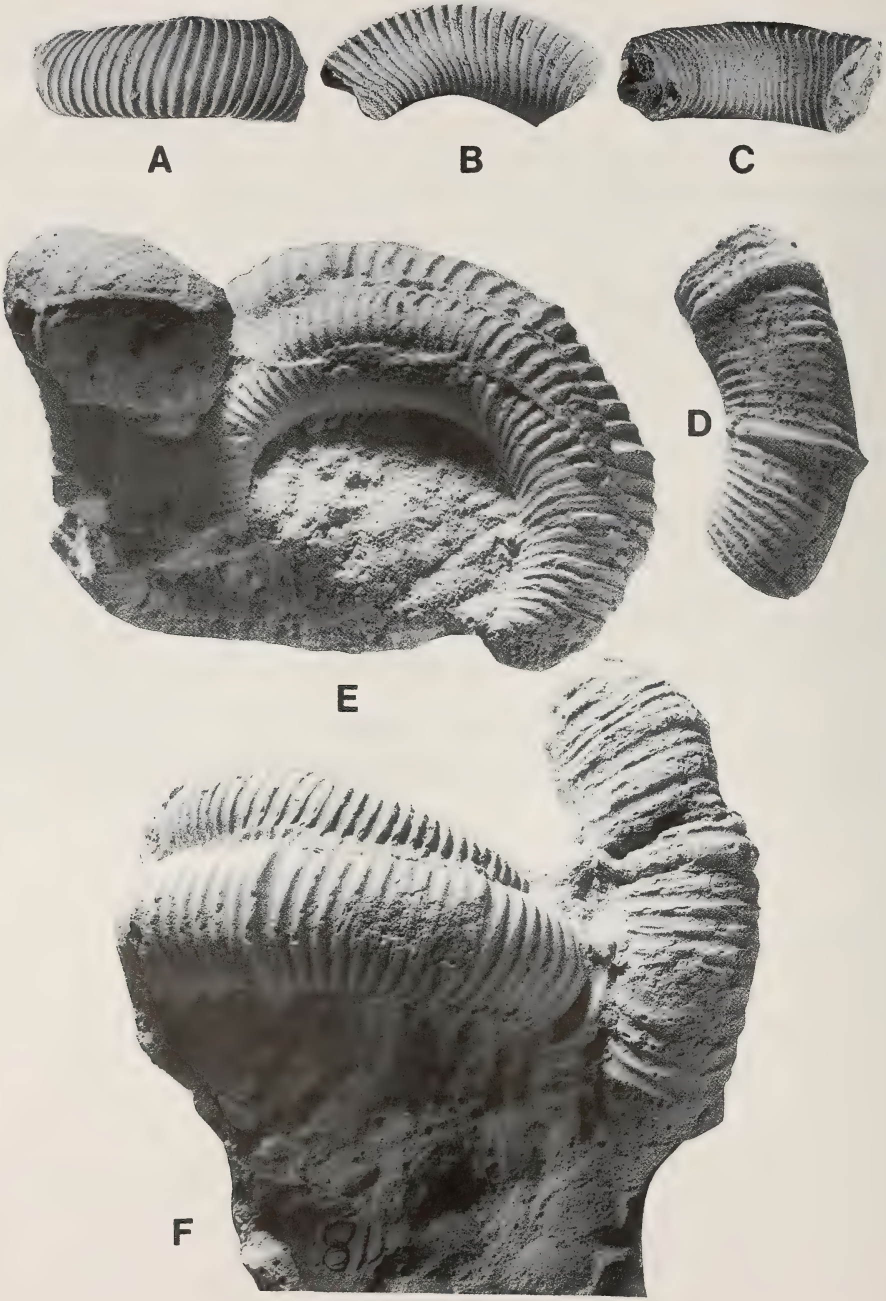

Figure 5

1983 *Hyphantoceras*(?) *amapondense* (van Hoepen); Lewy, p. 24, figs 1–6.
1985 *Hyphantoceras (?Madagascarites) amapondense* (Van Hoepen); Klinger, p. 6, figs 4i–K.
1987 *Hyphantoceras (?Madagascarites) amapondense* (van Hoepen); Immel, p. 134.
1991*a* *Hyphantoceras*(?) *amapondense* (van Hoepen); Kennedy & Cobban, p. 181, fig. 9: 9,10.
1995 *Hyphantoceras*(?) *amapondense* (Van Hoepen); Kennedy, p. 428, pl. 28 (figs 24–30).
1997 *Eubostrychoceras (Amapondella) amapondense* van Hoepen; Klinger & Kennedy, p. 244, figs 12–14A, 15A–D, 17A–C.

Type

Holotype by original designation is the specimen figured by Van Hoepen (1921, pl. 4 (figs 1–2)) in the Transvaal Museum Collections (Fig. 5E–F) from an unspecified horizon at locality 1, Mzamba River Estuary, Pondoland, Eastern Cape Province, Mzamba Formation, Santonian III?.

Material

A cast of the holotype, SAM-PCZ18722, from an unknown horizon at locality 1, Pondoland, Eastern Cape Province, Mzamba Formation, Santonian III?, also CGH (= SAM–PCP12882), SAM–PCP6890, SAM–PCP6891, SAM–PCP17368, SAM–13227, SAM–PCZ18729, SAM–PCZ18725, SAM–PCP18724, SAM–PCP18723, SAM–4821, SAM–PCP18726 SAM–PCP18721, SAM–7060, SAM–7061, all also from an unspecified horizon at locality 1; SAM–PCP8277, SAM–6890, SAM–8285, from Bed 7 at locality 1, Santonian III; SAM–PCZ7318, SAM–PCZ7321, SAM–PCZ7328, SAM–PCZ7342, SAM–PCZ17372 (ex Z2071) loose at locality 105, KwaZulu, St Lucia Formation, Santonian III or Campanian I; SAM–PCZ12881 (ex H126E/1), SAM–PCZ18719 from bed 5 at the same locality, Campanian I; SAM–PCZ18730 (ex H125) from locality 107, KwaZulu, St Lucia Formation, Campanian I; SAM–PCZ18727 (ex H77/H1) from locality 75, KwaZulu, St Lucia Formation, Santonian; SAM–PCZ18728 (ex H36/2) from locality 31, KwaZulu, St Lucia Formation, Santonian; SAM–PCF18720, SAM–PCF17338 (ex Collignon Collection) from Madagascar.

Description

Coiling is helical in the major part of the shell, forming a low spire with the whorls either just touching or slightly impressed; part of the body chamber curves upward, and over the apex of the helix. Ornament in the early stages consists of single ribs only; in later stages of the phragmocone and body chamber flared ribs occur between normal ribs.

Fig 5. (*see facing page*). *Eubostrychoceras (Amapondella) amapondense* (Van Hoepen, 1921). A–C. SAM–PCP18721 from locality 1, the Mzamba Estuary, Eastern Cape Province, Mzamba Formation, upper Santonian or lower Campanian. D. SAM–PCF17338 (ex Collignon Collection) labelled '*Hyphantoceras*' from Mitraiky, north of Manimbilo, Madagascar, Santonian. E–F. SAM–PCP18722. Cast of the holotype, Transvaal Museum collections from an unspecified horizon at the type locality of the Mzamba Formation at the Mzamba River Estuary, Eastern Cape Province, upper Santonian or lower Campanian. All × 1.

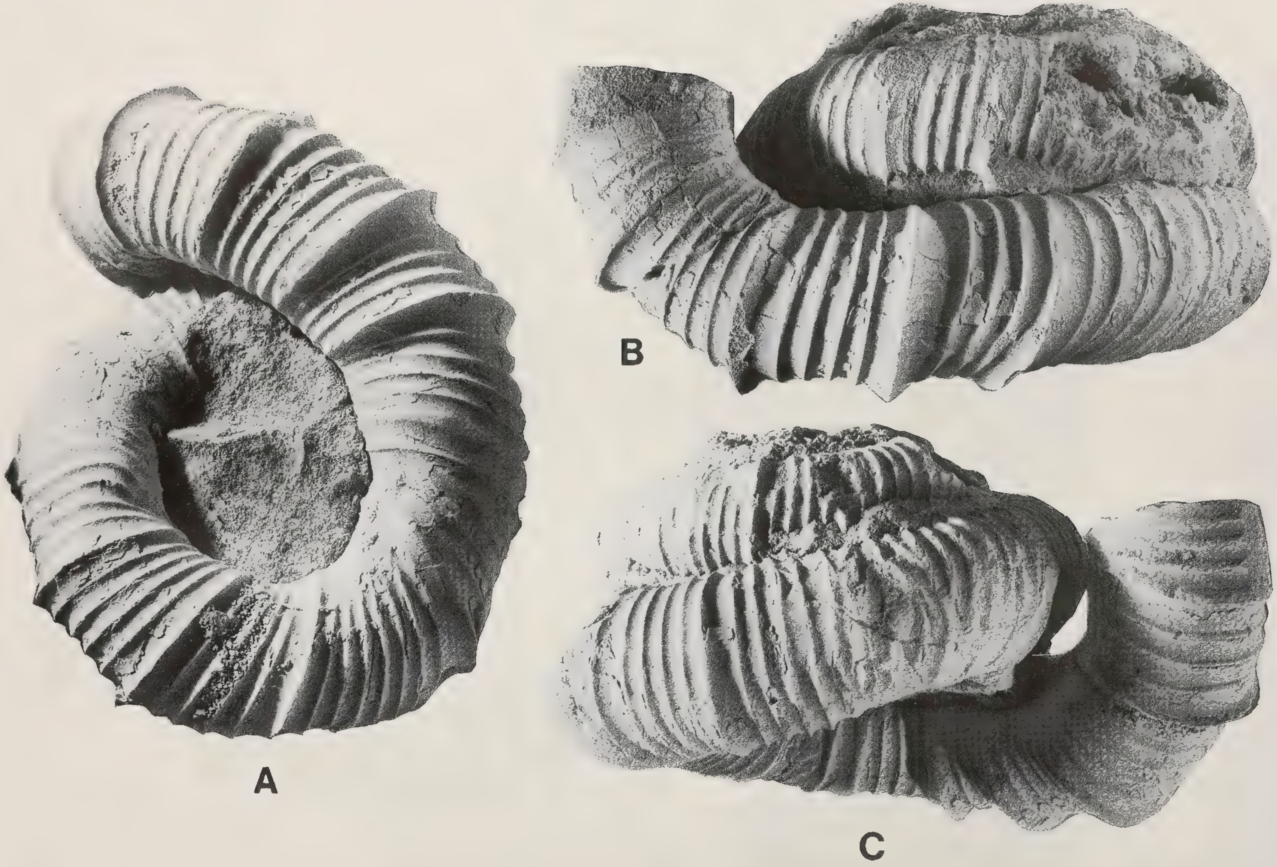

Figure 6

Eubostrychoceras (Amapondella) amapondense (Van Hoepen, 1921). SAM–PCZ7328 from locality 105, KwaZulu, St Lucia Formation, Campanian I. × 1.

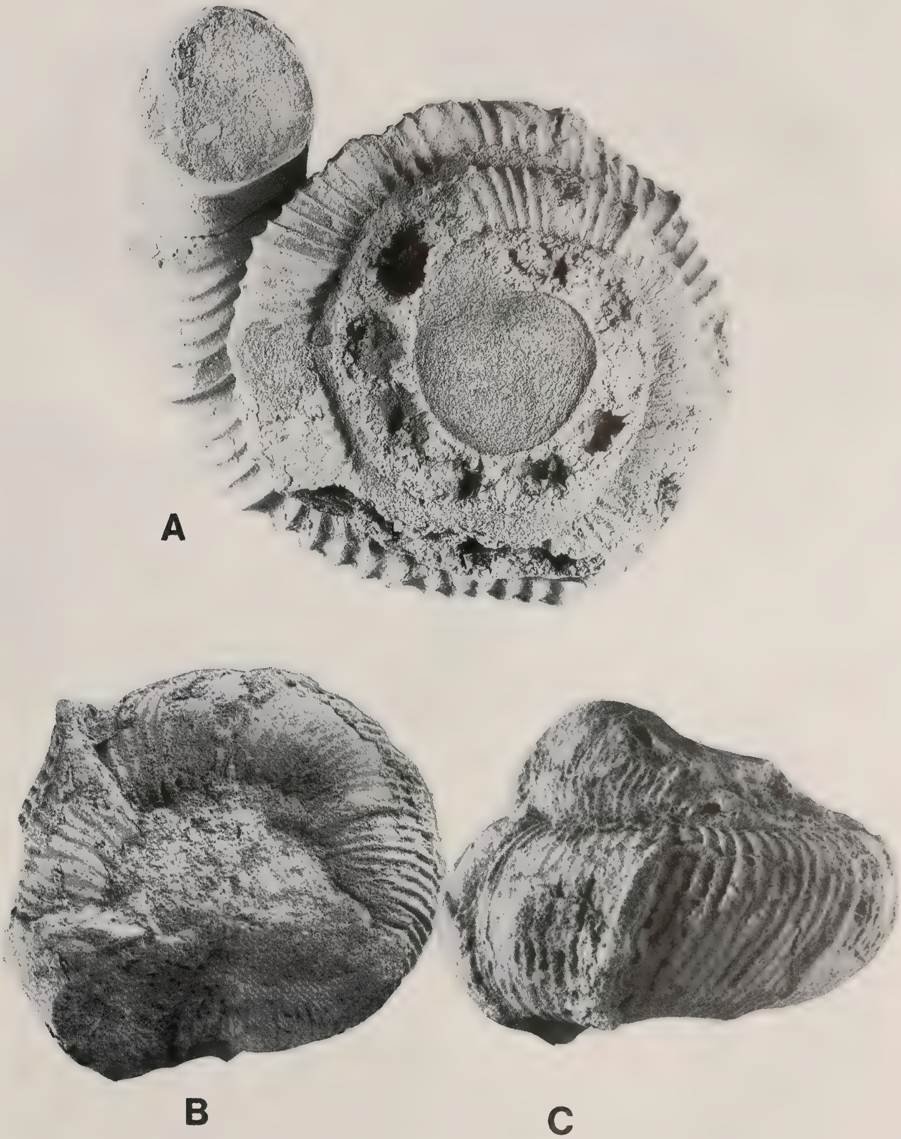

Figure 7

A. *Eubostrychoceras (Amapondella) amapondense* (Van Hoepen, 1921). SAM–PCZ7328 from locality 105, KwaZulu, St Lucia Formation, Campanian I. B–C. *Eubostrychoceras (E.) auriculatum* (Collignon, 1965). SAM–PCF17370 (ex Collignon collection) from Gisement 335, Beantaly (Belo sur Tsiribihina), Madagascar, lower Coniacian. Both × 1.

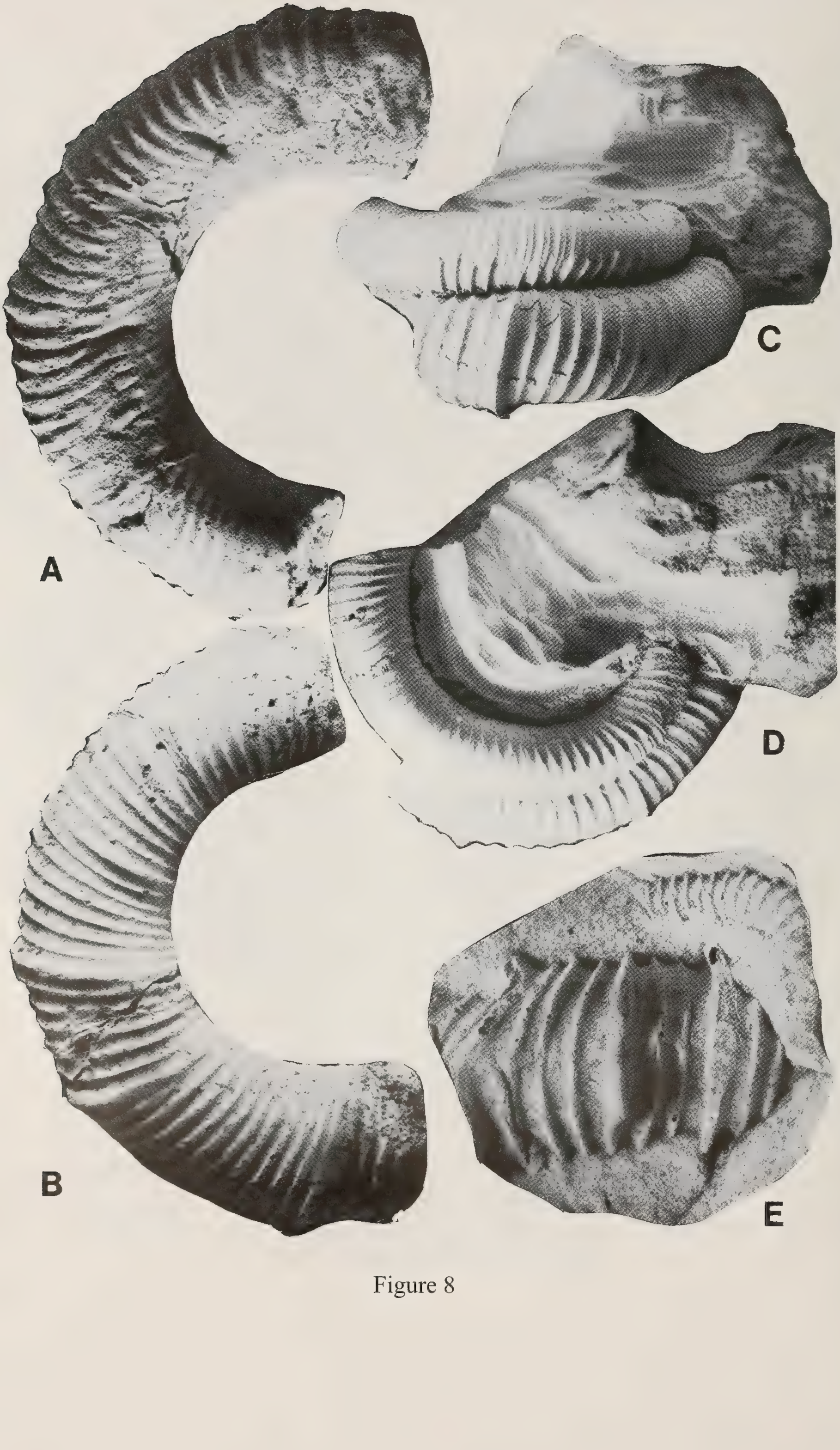

Figure 8

Discussion

This species is quite variable in overall size, tightness of coiling, and the stage at which flared ribbing first appears. Since Klinger's (1976) description of the species from Pondoland and KwaZulu, and inclusion of the Madagascan *Anaklinoceras*? *stephensoni* Collignon (1969: 50, pl. 532 (fig. 2096)) in its synonymy, *E. (A.) amapondense* has been recorded from the offshore deposits off the Natal South Coast (Klinger 1985), the upper Santonian of the Gosau Basin of Austria (Summesberger 1979, 1980; Immel 1987) (although Kennedy & Cobban 1991: 182 suggest that it may belong to *Jouaniceras sicardi* (De Grossouvre)), upper Santonian of France (Kennedy 1995), the upper Santonian of Israel (Lewy 1983), and Mississippi (Kennedy & Cobban 1991). We have also seen a specimen from the middle Santonian of Madagascar in the Collignon collection in Dijon.

The description of this latter material, especially that from Israel and additional material from Pondoland and KwaZulu clearly show that *Hyphantoceras* sp. A of Klinger (1976: 32 (figs 2–4), pl. 33 (fig. 1a–b)) is a synonym of *E. (A.) amapondense*. Klinger (1976: 71) admitted that *Hyphantoceras* sp. A and *E. (A.) amapondense* were practically indistinguishable in small fragments, but thought that the former differed on account of the tighter coiling and ovoid whorl section. We agree with Lewy (1983: 25) that these differences are within the range of variation of *E. (A.) amapondense*.

Some of the Campanian Madagascar specimens identified by Collignon (1969: 38, pl. 527 (fig. 2079–2080)) as *Hyphantoceras reussianum* (d'Orbigny, 1850)—a typical Turonian species, are also parts of *E. (A). amapondense*. But *H. reussianum* in Collignon (1969: 29, 523 (fig. 2064)) is different. According to Matsumoto (1977: 308) it may be an example of *Ainoceras* Matsumoto & Kanie, 1967. An alternative explanation is that it could be a coarsely ribbed *E. (Eubostrychoceras)*—allied perhaps to *E. (E.) junior* (Moberg, 1885). Undescribed specimens labelled as '*Hyphantoceras*' (ex Collignon collection) from the Santonian of Mitraiky, Madagascar (Figs 5D, 9A) also belong to *E. (A.) amapondense*.

The specimen from Mkweyane (Umkwelane Hill) described and figured by Spath (1921*a*: 255, pl. 24 (fig. 2)) as *Bostrychoceras*? sp. ind. also belongs to *E. (A.) amapondense*. It is on the same block of matrix from which *Diaziceras tissotiaeforme* Spath (1921*a*: 245, pl. 19 (fig. 1a–c)) was extracted. Spath also described several fragments as *Bostrychoceras*? sp. nov., which he considered to be the same as Woods' (1906, pl. 42 (fig. 5a–b)) specimen. The latter is unquestionably *E. (A.) amapondense*, but Spath's

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Fig 8. (*see facing page*). A–D. *Eubostrychoceras (Amapondella) amapondense* (Van Hoepen, 1921). A–B. SAM–PCZ12881 (ex H126E/1) from Bed E at locality 105, KwaZulu, St Lucia Formation, Campanian I. C–D. SAM–PCP12882 (ex CGH) from an unspecified horizon at the type locality of the Mzamba Formation at the Mzamba Estuary, Eastern Cape Province, Mzamba Formation, upper Santonian or lower Campanian. E. *Didymoceras (Eodidymoceras)*? sp. SAM–PCZ12949 (ex SAS–Z2071), latex peel showing apparent hamitid early whorls and part of body chamber with bituberculate, flared ribs. From an unspecified horizon at locality 105, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian. All × 1.

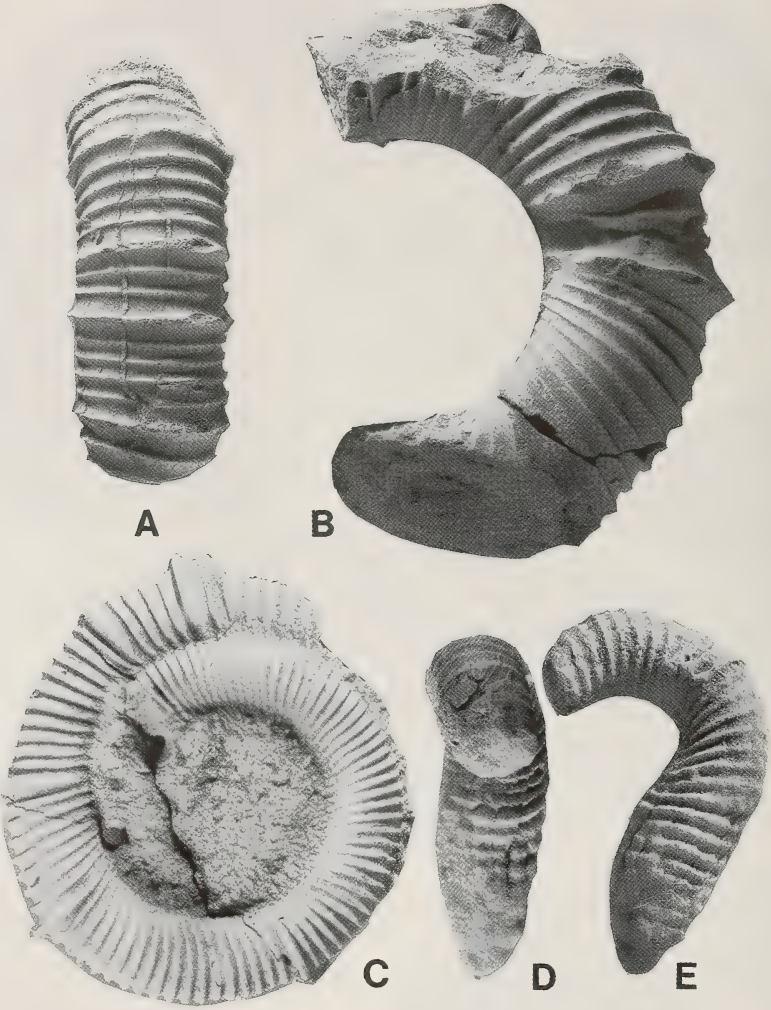

Figure 9

A–C. *Eubostrychoceras (Amapondella) amapondense* (Van Hoepen, 1921). A. SAM–PCF18720 (ex Collignon collection), labelled *'Hyphantoceras'* from Gisement 252, Coupe de Bevaho, (Belo sur Tsiribihina), Madagascar, lower Campanian, Zone of *Anapachydiscus wittekindi* and *Eulophoceras jacobi*. B. SAM–PCZ18719 from locality 105, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian. C. SAM–PCP6890 from Bed 7 at locality 1, Eastern Cape Province, Mzamba Formation, Santonian III. D–E. *Eubostrychoceras (Eubostrychoceras?)* sp. SAM–PCZ18750 from locality 105, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian. All × 1.

specimens include parts of straight shafts—e.g. SAM–PCZ18739 and are best referred to *Glyptoxoceras*.

Complete or semi-complete specimens of *E. (A.) amapondense* are rare. However, examination of the holotype and SAM–PCP12882 from Pondoland, SAM–PCZ7328, SAM–PCZ18727 (ex H77/hi) and SAM–PCZ18728 (ex H36/2) from KwaZulu, the holotype of *Anaklinoceras*? *stephensoni* from Madagascar and the specimen from Israel figured by Lewy (1983, figs 1–6) show the range of variation in overall size, tightness of coiling, apical angle of the helix and the stage at which flared ribbing first appears.

The near-complete Israeli specimen and SAM–PCP12882 (CGH) are more or less the same size; yet in the former, flared ribs already occur on the third-last whorl of the helix, whereas the Pondoland specimen only has flared ribbing on the last whorl of the helix. The Israeli specimen also has a lower apical angle. This early onset of flared ribbing corresponds more or less to Klinger's *Hyphantoceras* sp. A., which, as discussed above, is a synonym of *E. (A.) amapondense*. Lewy (1983, figs 4–6) figured the early helical whorls. These show the initial simple ribbing, but with onset of flared ribbing at a diameter of 16 mm. SAM–PCP6890 (Fig. 9C) has simple ribbing up to a diameter of 46 mm; flared ribs only appear beyond that diameter.

Cobban & Scott (1972: 46) compared *Puebloites spiralis* with Woods' (1906: 340, pl. 44 (fig. 3a–d)) *Hamites (Anisoceras)* sp. *Puebloites*, however, is much older (Cenomanian–Turonian) and never develops flared ribbing.

Ankinatsytes yabei Collignon (1965: 16, pl. 420 (fig. 1738)) from the lower Coniacian of Madagascar has ornament reminiscent of the later stages of *E. (A.) amapondense* with normal and flared ribs; but the latter are allegedly trituberculate. We can not say whether these two species are related or not.

Crioceras serta Müller & Wollemann (1906: 20, pl. 9 (fig. 3), pl. 10 (figs 1–3)) shows a similar ontogenetic sequence of ornament–simple ribbing on the early whorls followed by intercalated flared ribs on the outer whorls. Unfortunately all the German specimens are crushed, and the complete form of the shell is unknown. It could possibly also be referred to *E. (Amapondella)*. Collignon (1970: 15, pl. 613 (figs 2286–2288)) described and figured a helically coiled heteromorph from the middle Campanian of Madagascar as *Neoglyptoxoceras serta*. The Madagascan material, however, appears to have regular ribbing throughout, thus differing from the German *Crioceras serta*. The Madagascan material is here renamed *Neoglyptoxoceras collignoni* nom. nov. The holotype is the specimen figured by Collignon (1970, pl. 613 (fig. 2286)). (See also p. 311).

Occurrence

Upper Santonian Pondoland, offshore Natal South Coast, Austria, France and Mississippi, upper Santonian and lower Campanian, KwaZulu and middle Santonian to lower Campanian of Madagascar. Together with the texanitid genera *Submortoniceras* and *Reginaites*, *E. (Amapondella)* is a good indicator of the proximity of the Santonian–Campanian boundary in South Africa.

Genus *Nostoceras* Hyatt, 1894

Type species

Nostoceras stantoni retrorsum Hyatt (1894: 570) by the original designation of Hyatt (1894: 569).

Diagnosis

The major part of the phragmocone is coiled in a tight helix. Coiling changes in the later part of the phragmocone and body chamber. Ornament generally consists of two rows of tubercles at some stage; in some forms irregularly developed.

Discussion

In most *Nostoceras (Nostoceras)* species the body chamber forms a distinct U-shaped loop suspended below the base of the preceding spire, with the aperture often very close to the latter. *N. (N.) liratum* Kennedy 1992*b* is an exception. Here, the body chamber curves upwards, in contact with the helix. This is reminiscent of *E. (Eubostrychoceras)*, or possibly transitional to *N. (Anaklinoceras)* Stephenson, 1941 (type species *Anaklinoceras reflexum* Stephenson, 1941). In *Nostoceras (Anaklinoceras)* the body chamber curves upwards and over the apex of the helix and the shells are generally small. In *Nostoceras (Planostoceras)* Lewy, 1967 (type species *Planostoceras rehavami* Lewy, 1967) the body chamber forms a hook at right angles to the axis of coiling of the helix and parallel to the base of the latter. In *Nostoceras (Bostrychoceras)* the body chamber also forms a loop suspended below the base of the spire as in *Nostoceras* s.s., but is generally larger, and with irregular tuberculation. In *N. (Pravitoceras)* Yabe, 1902 (type species *Pravitoceras sigmoidale* Yabe, 1902) the terminal hook is in the same plane as the predominantly planispiral phragmocone and is C-shaped, involving a 180° torsion of the shell.

Occurrence

Campanian to Maastrichtian.

Subgenus *Nostoceras (Nostoceras)* Hyatt, 1894

Type species

Nostoceras stantoni retrorsum Hyatt (1894: 570) by original designation of Hyatt (1894: 569).

Diagnosis

The major part of the phragmocone consists of a closely coiled helix, either dextral or sinistral, generally with an acute apical angle, followed by a U-shaped, retroversal body chamber hook which brings the aperture to a position just below the base of the helical stage. Ornament consists of ribs with one or two rows of tubercles; some have no tubercles at all.

Occurrence

Upper Campanian and Maastrichtian. *Nostoceras (Nostoceras)* is best known from North America (Gulf Coast, Atlantic Sea Board and Western Interior), but has also been reported from Colombia (in Cobban 1974: 8), Peru, Argentina, Angola, Nigeria, Libya, Egypt, Israel, Madagascar, KwaZulu, and various regions in Europe including England, Spain, France, Belgium, The Netherlands, Italy, Poland, Ukraine, Austria, Bulgaria, and Russia; and Australia, India and Japan.

Nostoceras (Nostoceras) subangulatum Spath, 1921
Fig. 10A

1921*a* *Nostoceras*? *subangulatum* Spath, p. 250, pl. 22 (fig. 3a–c).

Type

Holotype by monotypy is SAM–PCZ18731 from east of the Railway at Riverview Halt, KwaZulu, St Lucia Formation, probably Campanian.

Discussion

No additional specimens of this species have been found and the holotype is here figured (Fig. 10A) for comparison with the holotype of *N. (N.) natalense* which was recorded from the same locality. The ornament of the two species is broadly comparable; both have a large row of tubercles situated just above midflank and a second row at the base of the spire, just visible above the suture between the whorls. The whorl section in *N. (N.) natalense* is more angular, and the apical angle is much larger, resulting in a low, squat spire. In contrast, *N. (N.) subangulatum* has a rounded whorl section and a much smaller apical angle, resulting in a shell shape reminiscent of the turrilitid genus *Mariella* Nowak, 1916 as was also noted by Spath (1921*a*: 252).

Occurrence

Probably Campanian, KwaZulu.

Nostoceras (Nostoceras) natalense Spath, 1921
Figs 10B–D, 11–12

1921*a* *Nostoceras*? *natalense* Spath, p. 248, pl. 22 (fig. 2a–b).
?1931 *Turrilites (Bostrychoceras) Schloenbachi* Favre; Basse, p. 19, pl. 2 (figs 11–15).
1965 *Nostoceras*(?) *obtusum* Howarth, p. 384, pl. 10 (fig. 2), text-fig. 17.
?1971 *Nostoceras obtusum* Howarth; Collignon, p. 9, pl. 643 (fig. 2375).
?1971 *Nostoceras hyatti* Steph.; Collignon, p. 8, pl. 643 (fig. 2371).
1976 *Didymoceras (D.) natalense* (Spath); Klinger, p. 68, pl. 30 (fig. 3), pl. 31 (figs 1–3), pl. 32 (fig. 1).

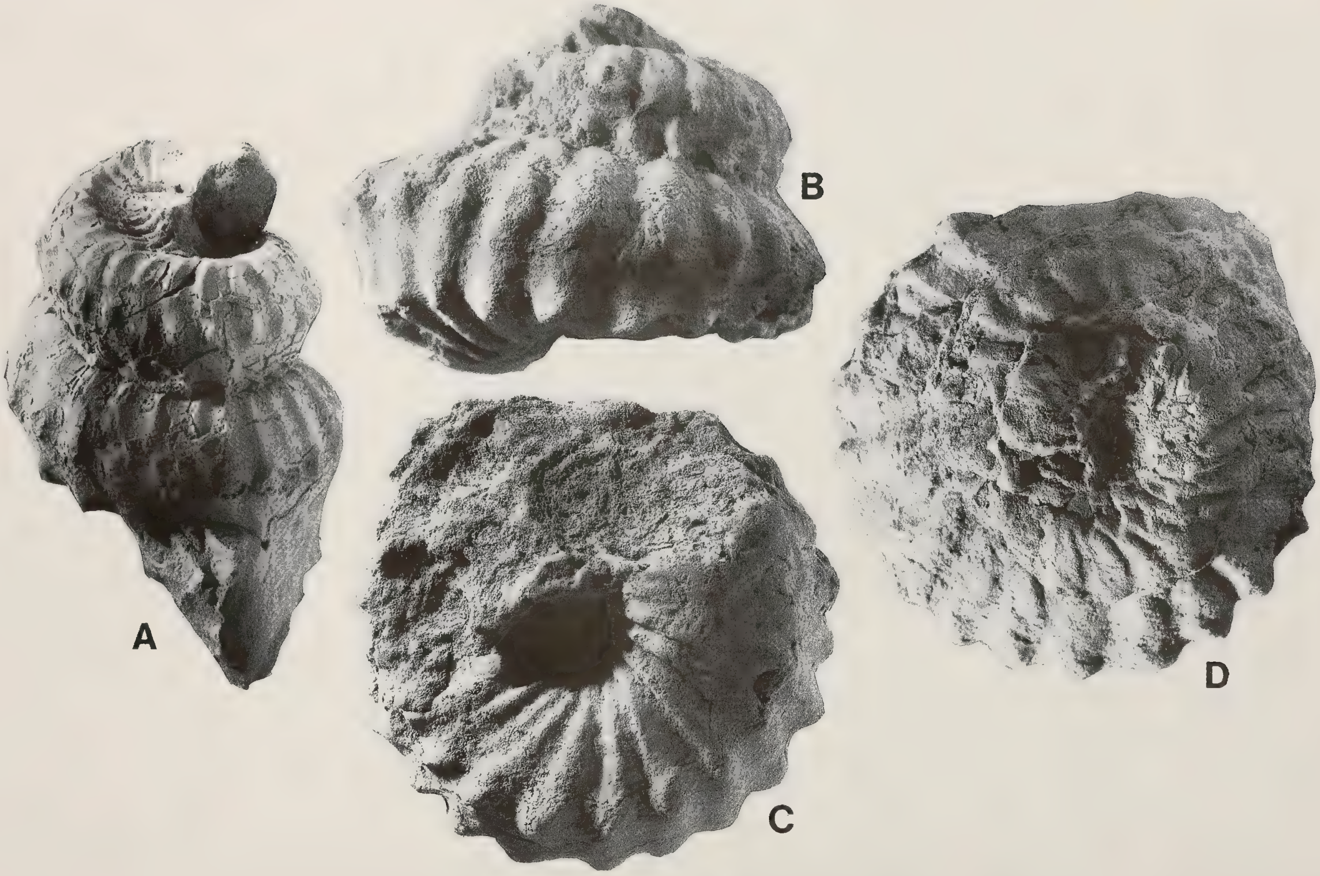

Figure 10

A. *Nostoceras (Nostoceras) subangulatum* Spath, 1921. SAM–PCZ18731, the holotype. B–D. *Nostoceras (Nostoceras) natalense* Spath, 1921. SAM–PCZ18732, the holotype. Both from east of the Railway at Riverview Halt, KwaZulu, St Lucia Formation, probably upper Campanian. Both × 1.

Type

Holotype by monotypy is SAM–PCZ18732 from east of Riverview Railway Halt, KwaZulu, St Lucia Formation, probably Campanian.

Material

SAM–PCZ18733, SAM–PCZ18734 from locality 113, KwaZulu, St Lucia Formation, Maastrichtian a or b; SAM–PCZ18736 (ex Z2270) and SAM–PCZ18735 (ex H106) from locality 117, KwaZulu, St Lucia Formation, Maastrichtian a, SAM–PCZ18737 (ex H116/2) from locality 120, KwaZulu, St Lucia Formation, Maastrichtian a.

Description

Apart from SAM–PCZ18734 (Fig. 11F), no further material has been found since Klinger's (1976) description. The five available specimens show considerable variation. At one end of the scale is a coarsely ornamented form with an apical angle of about 70° as in the holotype (Fig. 10B–D). The ribs on the adapical part of the whorls are broad and strong and incipiently looped in the early whorls. They are connected to large tubercles situated above mid-flank, then weaken on the flank before connecting to a smaller, abaperturally displaced row of smaller tubercles visible just above the whorl suture. The ribs continue over the base of the spire in a prorsiradiate fashion, narrowing towards, and continuing over the whole of the umbilical wall.

The other end of the scale is typified by SAM–PCZ18736 (Fig. 11A) with a wide apical angle of about 130°. Here the adapical part of the whorl is ornamented by much finer ribs and these connect in unequally strong pairs to the upper row of tubercles, which are situated in the whorl suture.

Specimens such as SAM–PCZ18734 (Fig. 11F) and SAM–PCZ18737 (Fig. 11C–E) connect these two extremes of variation. In both, the ribbing is coarser than in SAM–PCZ18736 but still distinctly looped on the upper and lower parts of the whorls. SAM–PCZ18735 (Fig. 11B) consists of the last part of the helix and the retroversal body chamber. A single constriction is present in SAM–PCZ18737 (Fig. 11C–E).

Discussion

Klinger (1976: 68) regarded the Angolan *N. (N.) obtusum* (Howarth 1965: 384, pl. 10 (fig. 2), text-fig. 17) as a synonym of *N. (N.) natalense*. When compared with the holotype, Howarth's (1965: 384) reasons for maintaining them separate—e.g. large tubercle, bold ribs and smaller umbilicus—seem reasonable. However, SAM–PCZ18734 (Fig. 11F) has an apical angle, open umbilicus and rib density indistinguishable from the holotype of *N. (N.) obtusum*, and we consider *N. (N.) natalense* to be a senior synonym of *N. (N.) obtusum*.

All the specimens described by Basse (1931: 19, pl. 2 (figs 11–15)) as *Turrilites (Bostrychoceras) schloenbachi* are smaller than our smallest specimen. They definitely do not belong to Favre's (1869) *N. (N.) schloenbachi* (see Kennedy & Summesberger 1987: 30–31 for a review of that species). The largest of Basse's specimens (1931, pl. 2 (fig. 15)), however, is very similar to SAM–PCZ18737 (Fig. 11C–E). The impression of

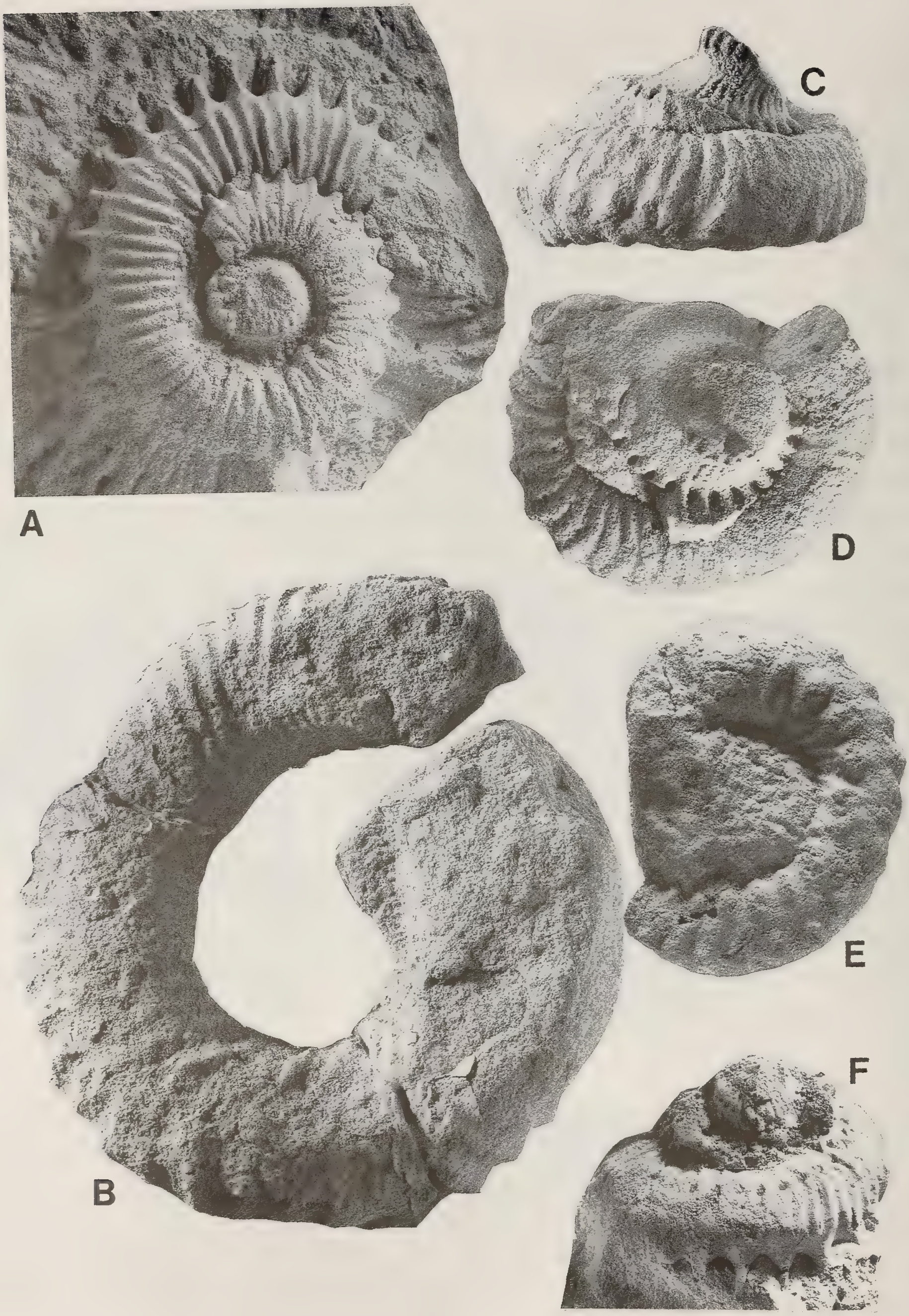

Figure 11

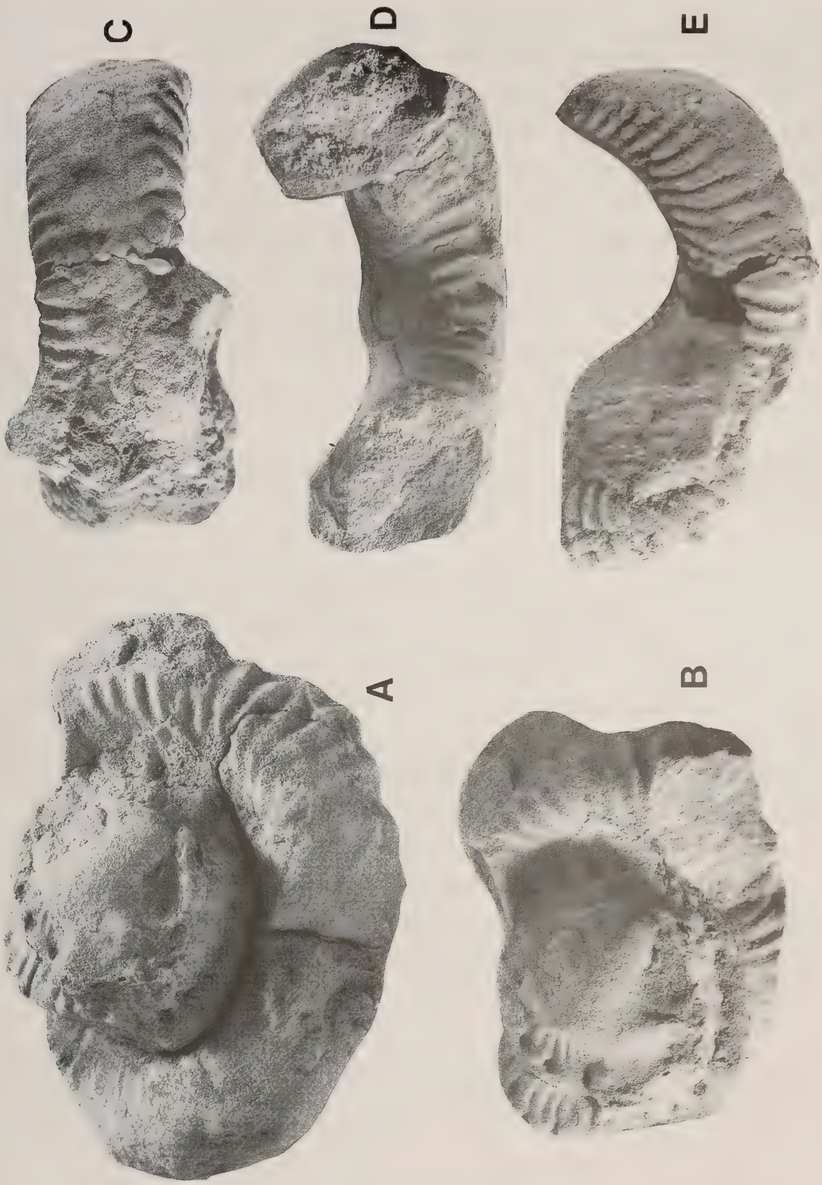

Figure 12

Nostoceras (Nostoceras) natalense Spath, 1921. SAM–PCZ18733 (ex 113). A–B. Complete specimen. C–E. Part of outer whorl removed. From locality 113, KwaZulu, St Lucia Formation, Maastrichtian a or b. Both × 1.

Fig. 11. (*see facing page*). *Nostoceras (Nostoceras) natalense* Spath, 1921. A. SAM–PCZ18736 (ex Z2270) from locality 117, KwaZulu. Specimen with distinct siphonal spines and bifurcating ribbing on the adapical side. B. SAM–PCZ18735 (ex H106) part of a recurved body chamber from the same locality as A. C–E. SAM–PCZ18737 (ex H116/2) from locality 120, KwaZulu. F. SAM–PCZ18734 from locality 113, specimen showing distinct abapical spines. All from the St Lucia Formation, Maastrichtian a or b. All × 1.

an earlier whorl on this specimen shows fine ornament comparable to that of Basse's material.

The specimens figured by Collignon (1971: 13, pl. 644 (figs 2385–2386)) as *Didymoceras schloenbachi* could also possibly be included in *N. (N.) natalense*, but they are too small for definite allocation. At any rate, they also do not belong to Favre's species.

Nostoceras obtusum Howarth in Collignon (1971: 9, pl. 643 (fig. 2375)) from the lower Maastrichtian of Mont Ambohitsiombe, Madagascar is very similar to the KwaZulu specimen SAM–PCZ18737 (Fig. 11C–E) and is also tentatively referred to *N. (N.) natalense.*

Another specimen figured by Collignon (1971: 8, pl. 643 (fig. 2371)) as *Nostoceras hyatti* Stephenson is possibly also a *N. (N.) natalense*, comparable to the finely ribbed forms, e.g. SAM–PCZ12942 (Fig. 11A).

Our finer ribbed specimen, SAM–PCZ18736 (Fig. 11A) resembles some *Nostoceras (N.) alternatum* (Tuomey, 1851) as figured by Cobban (1974: 86, figs 1w–rr, 5) and Cobban & Kennedy (1991: E3, pl. 2 (figs 5–27)). This species has a similar prominently pointed row of upper tubercles connected by looped ribs on the adapical edge. Generally, however, it seems to have a larger apical angle (45–90°) and a higher spire–compare e.g. Cobban's (1974, fig. 5) restoration of *N. (N.) alternatum* with SAM–PCZ18736 (Fig. 11A). Some specimens, e.g. Cobban & Kennedy (1991, pl. 2 (figs 12–13)) with a wide apical angle are indistinguishable from SAM–PCZ18736. The similarity between *N. (N.) alternatum* and *N. (N.) obtusum*, the latter here regarded as a synonym of *N. (N.) natalense*, was also noted by Cobban & Kennedy (1991: E3) and Cobban (1974: 87). Given more material, *N. (N.) natalense* and *N. (N.) alternatum* may eventually turn out to be the same, or possibly only different subspecies.

Küchler & Odin (2001: 509) commented on the similarities between *Nostoceras (N.) obtusum* and *N. (N.) schloenbachi* (Favre, 1869), but separated the latter on account of the more rounded whorl section and coarser ribs and/or much coarser tubercles.

Occurrence

Maastrichtian a or b KwaZulu, lower Maastrichtian Madagascar, Campanian/ Maastrichtian, Angola, uppermost Campanian of Tercis, France (as *N. (?D.) obtusum* (Küchler & Odin 2001: 507)).

Subgenus *Nostoceras (Bostrychoceras)* Hyatt, 1900

Type species

Turrilites polyplocus Roemer (1841: 92, pl. 14 (figs 1–2)), by original designation of Hyatt (1900: 588).

Diagnosis

Coiling helical, initially ornamented by fine ribs and two rows of tubercles; later tuberculation may become irregular or disappear completely. Body chamber forms distinct loop below the spire.

Discussion

Virtually all the species that had originally been referred to *Bostrychoceras* have now been placed in *Eubostrychoceras*. Simply put, tight, helically coiled specimens with tubercules at some stage of their ontogeny are referred to *Nostoceras (Bostrychoceras)*, whereas those predominantly without tubercles are referred to *Eubostrychoceras (Eubostrychoceras)*. Kennedy (1986) examined several specimens of the type species of *N. (Bostrychoceras)* and illustrated the extreme degree of variation, thus eliminating the need for the various names created by Wiedmann (1962), Blaszkiewicz (1980) and recently Küchler (2000).

Occurrence

Upper Campanian and lower Maastrichtian, Europe, Texas and Angola.

Nostoceras (Bostrychoceras) sanctaeluciense Klinger, 1976

Figs 13–40, 47D

?1909 *Anisoceras notabile* Whiteaves sp.; Kilian & Reboul, p. 15 (*pars*), pl. 5?, pl. 6 (fig. 1 only).

1976 *Didymoceras (Didymoceras) depressum* (Wiedmann) *sanctaeluciense* Klinger, p. 65, pl. 25–28, pl. 29 (figs 1–3), pl. 30 (figs 1–2), text-figs 8f–h.

Type

Holotype (Figs 13–16) by original designation of Klinger (1976) is SAS–Z762 from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b.

Material

In addition to the original material in the collections of the Council for Geosciences we have numerous specimens from the following localities: SAS–Z2251, SAM–PCZ9028, SAM–PCZ9079, SAM–PCZ9328, SAM–PCZ9334, SAM–PCZ9339, SAM–PCZ10494 from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b; SAM–PCZ9329, SAM–PCZ9335, SAM–PCZ9340, SAM–PCZ9342, SAM–PCZ9343, SAM–PCZ17341 (ex H116/7), SAM-PCZ17349 (ex H115/15) SAM–PCZ17350,(ex 115/13) from locality 120, KwaZulu, St Lucia Formation, Maastrichtian a or b; SAM–PCZ10489, SAM–PCZ10490, SAM–PCZ10493, SAM–PCZ10497, SAM–PCZ10500, SAM–PCZ10501, SAM–PCZ10502, SAM–PCZ10505-10507, from locality 125, KwaZulu, St Lucia Formation, Maastrichtian a or b; SAS–A2009, SAM-PCZ7907, SAM–PCZ9330, SAM–PCZ9331, SAM–PCZ9339, SAM–PCZ9431, SAM–PCZ10495, SAM–PCZ10496, SAM–PCZ10498 (ex A2016), SAM-PCZ10499 from locality 113, KwaZulu, St Lucia Formation, Maastrichtian a or b; SAM–PCZ7902, SAM–PCZ7927, SAM–PCZ10504, SAM–PCZ10606, SAM–PCZ17343–17346, SAM–PCZ17349, unlocalized from 'The Coves', localities 118–120, KwaZulu, St Lucia Formation, Maastrichtian a or b.

Diagnosis

Relatively large; low-spired phragmocone, ornamented by 100 to 130 ribs per whorl,

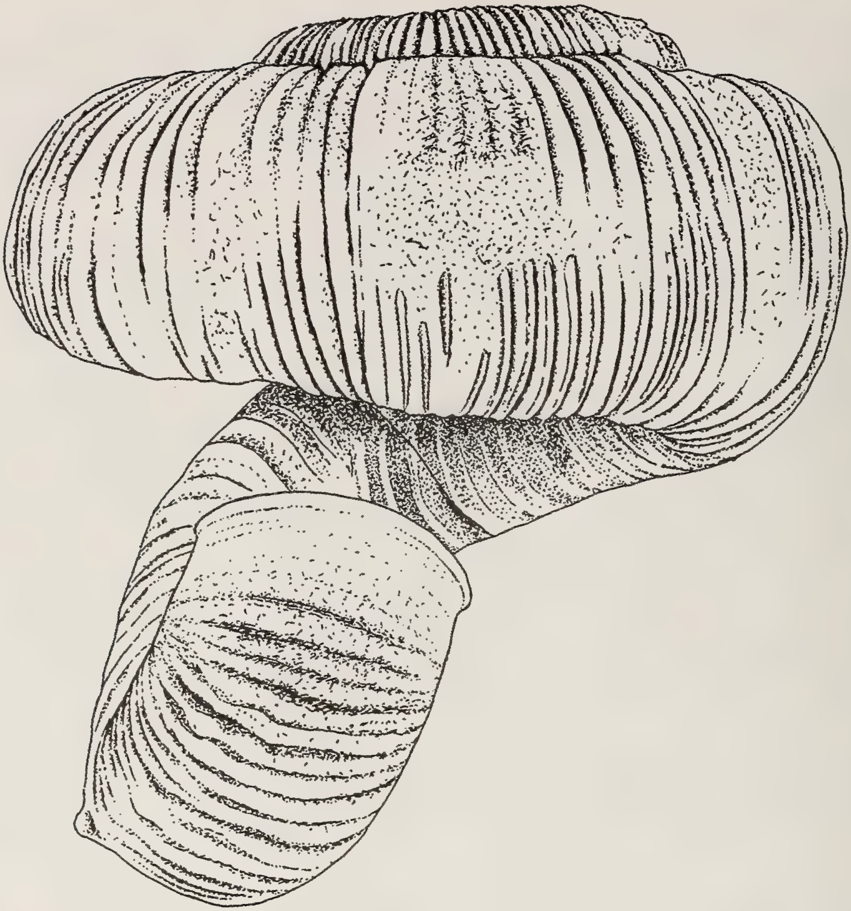

Figure 13

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). Stipple drawing by Samantha Black of the holotype, SAS–Z762 from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b. × 0.7

siphonal and abapical tubercles at some stage; the former disappear at larger diameters. Retroversal body chamber suspended below spire and ornamented irregularly by one or two rows of tubercles.

Description

Klinger (1976) described the species in detail, noting the variation in ornamentation on the phragmocone and on the body chamber. The new material includes specimens showing parts of the very early ontogenetic stage and others showing a wide range in overall size and variation in coiling of the phragmocone as well as the body chamber.

The earliest ontogenetic stage is shown in SAM–PCZ10490a, b (Fig. 17A, C), part and counterpart, consisting of four complete whorls. Coiling is very shallow, nearly planispiral. On the innermost whorl, 32 single, sharp ribs occur. On the second whorl, at a spiral diameter of *c.* 18 mm, spinose siphonal tubercles appear in the umbilical suture, either from single or from paired ribs—their tips resting on the adapical shoulder of the succeeding whorl. Distinct but small tubercles also occur on the inner abapical edge of the third whorl; here rib density has increased to about 80. On the outer whorl, rib density is about 100 to 120. The majority of ribs are single, but some are bifurcate on the inner third of the adapical edge.

Another specimen, SAM–PCZ10489a and b, part and counterpart (Figs 17B, 18B) also shows the early ontogenetic stage. Here, distinct abapical tubercles are visible at a spiral diameter of 25–30 mm. Three to four single ribs occur between these tubercles. In SAM–PCZ10499 (Fig. 19A–B) impressions of siphonal tubercles are still visible at a spiral diameter of 65 mm. On the next whorl, at a diameter of 95 mm, the siphonal tubercles have disappeared, but abapical tubercles are well developed. In SAM–PCZ10495 (Fig. 20) the outermost whorl shows distinct impressions of siphonal tubercles up to a diameter of about 80 mm, after which they disappear—thus confirming Klinger's (1976: 66) observations that siphonal tubercles only persist up to a maximum diameter of about 100 mm.

On internal moulds, ribbing is generally thin and thread-like on the phragmocone. In the original condition, however, the ribs were blade-like with rounded extremities, separated by wider interspaces. These interspaces are in-filled with calcitic matrix. When extracting specimens from the matrix, the layer consisting of the high ribs and interspace matrix usually detaches from the rest of the shell, resulting in a low-relief internal mould. In some specimens, e.g. SAM–PCZ10498 (Fig. 21B) and SAM–PCZ10503, part of the original high-crested ribbing is still preserved.

During ontogeny, the whorl section on the phragmocone changes from depressed (adapical-abapical) to rounded to distinctly laterally (dorsal-siphonal) compressed. Coiling in the phragmocone is both sinistral and dextral. In most specimens the apical angle is very wide, of the order of 120 to 140 degrees e.g. the holotype, SAS–Z762 (Figs 13–16), SAM–PCZ17341 (Fig. 21A), SAM–PCZ10494 (Fig. 22A), etc., but in some specimens, e.g. SAM–PCZ7927 (Fig. 22B), SAM–PCZ17343 (Fig. 22C), SAM–PCZ10493 (Fig. 22D), SAM–PCZ10506 (Fig. 23) and SAM–PCZ17352 (Fig. 47D), the spire is turreted with an acute apical angle of the order of 60 degrees.

The body chamber occupies approximately the last third to quarter (or even less) of a whorl of the spirally coiled section before it breaks away to form a retroversal loop. The whorl section of the body chamber in the spiral section is very characteristic in being high, laterally compressed and in having a distinct adapical zone of impression. The uncoiled section of the body chamber recurves, forming an angle of between 60 and 90 degrees with the base of the spire, and ends very close to the latter. The aperture is preserved in several specimens, e.g. SAM–PCZ10499, SAM–PCZ9328, SAM–PCZ10500 (Fig. 24) SAM–PCZ7902 (Fig. 25A), SAM–PCZ9336, SAM–PCZ10501 (Fig. 26) and SAM–PCZ10506, first forming a slight constriction and then a simple flare. Ornament on the body chamber is quite irregular, consisting of one or two rows of tubercles which are much larger than those of the phragmocone. There is usually a non-tuberculate interval

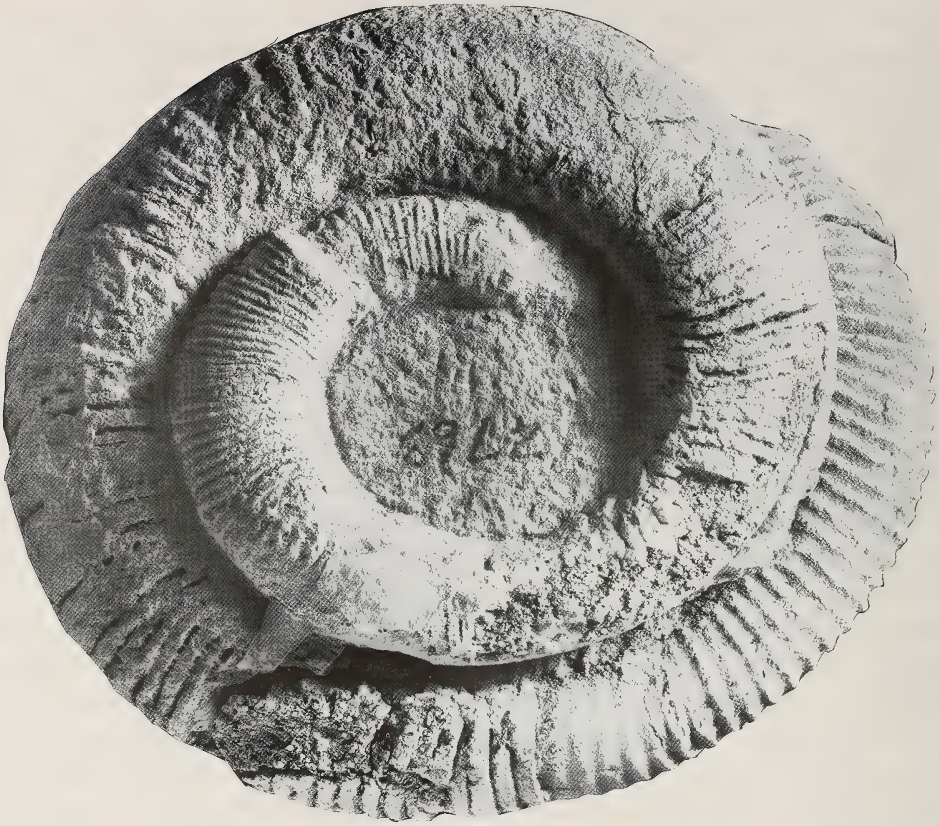

Figure 14

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). Apical view of the holotype, SAS–Z762 from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b. × 0.7.

between the last occurrence of tubercles on the spiral section, and the first appearance of tubercles on the body chamber. The suture line is extremely complex and interdigitated.

The species shows an extreme variation in size. This is very obvious by the different sizes of adult specimens with complete, recurved body chambers. In the smallest adult, SAM–PCZ9328 (Figs 29–30), the body chamber detaches itself at a whorl height (adapical-abapical diameter) of 40 mm, whereas the largest, SAM–PCZ17346 (Fig. 31 A–B) uncoils at a height of 85 mm. Other specimens uncoil at intermediate whorl heights:

SAM–PCZ10499–42 mm
SAM–PCZ10504–*c.* 50 mm
SAM–PCZ10506–55 mm
Holotype–*c.* 60 mm
SAM–PCZ10505–68 mm.

It is tempting to ascribe the variation in size at which maturity is attained to dimorphism—the small specimens are microconchs and the large ones macroconchs.

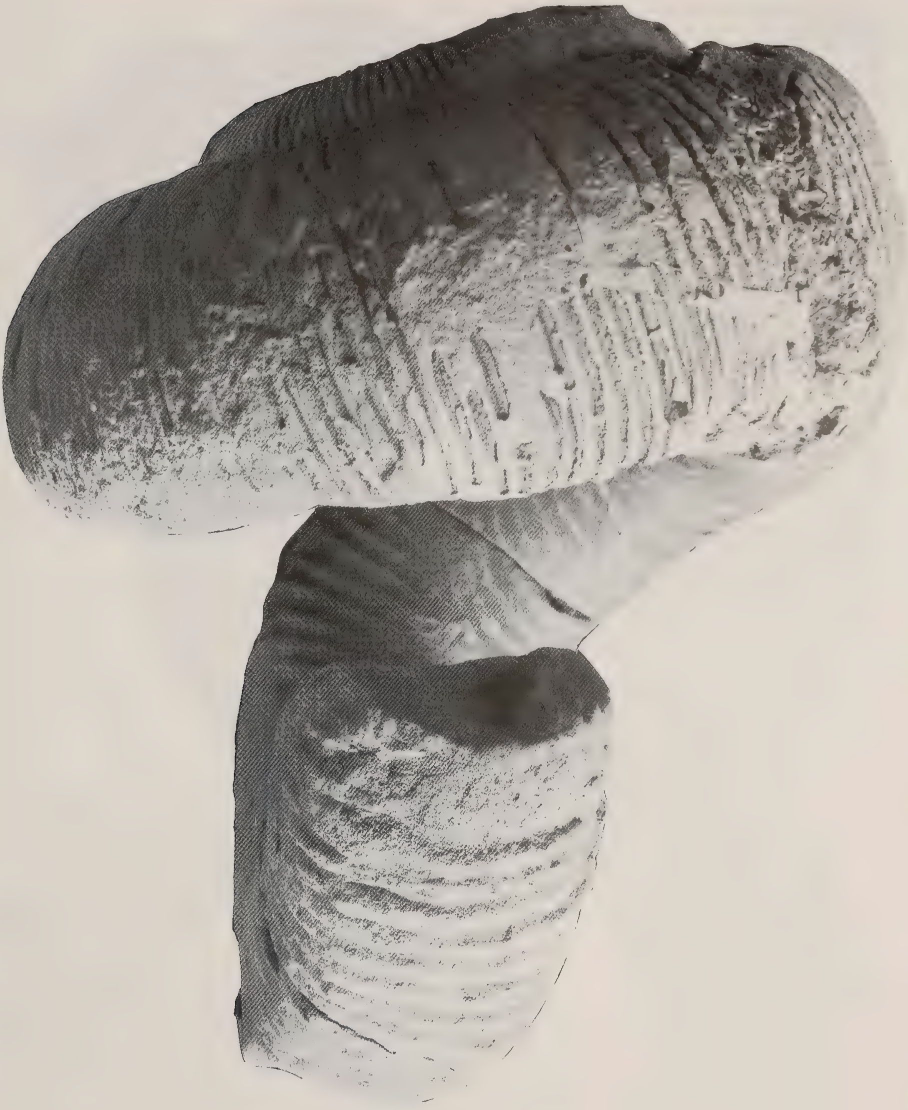

Figure 15

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). SAS–Z762, the holotype from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b. × 0.8.

However, as the dimensions indicate, there seems to be a nearly continuous growth series from smallest to largest. If this size difference is indeed due to dimorphism, there is a large degree of overlap in size between microconchs and macroconchs. There are, however, other differences between the small and large specimens. In the smallest specimens, the body chamber occupies very little of the spiral part of the shell. More important, perhaps, is the fact that the retroversal loop is suspended perpendicularly below the base of the

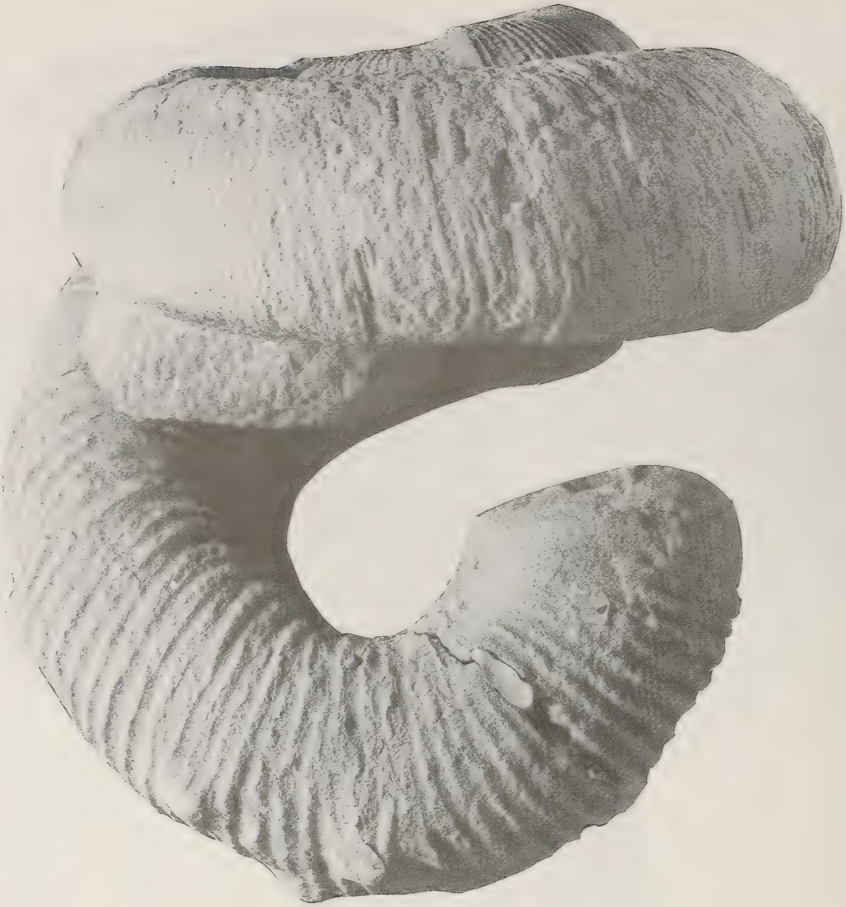

Figure 16

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). SAS–Z762, the holotype from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b. × 0.7.

Fig. 17. (*see facing page*). *Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). A, C. SAM–PCZ10490a, b, part and counterpart of the very early helical whorls. Note the very early onset of helical coiling and apparent absence of irregularly coiled early stage. From locality 125, KwaZulu. B. SAM–PCZ10489. Note the development of large, lateral spines on thickened ribs. From locality 119, KwaZulu. D. SAM–PCZ10496. Ventral view of part of phragmocone showing ventral tubercles. From locality 113, KwaZulu. All from the St Lucia Formation, Maastrichtian a or b. All × 1.

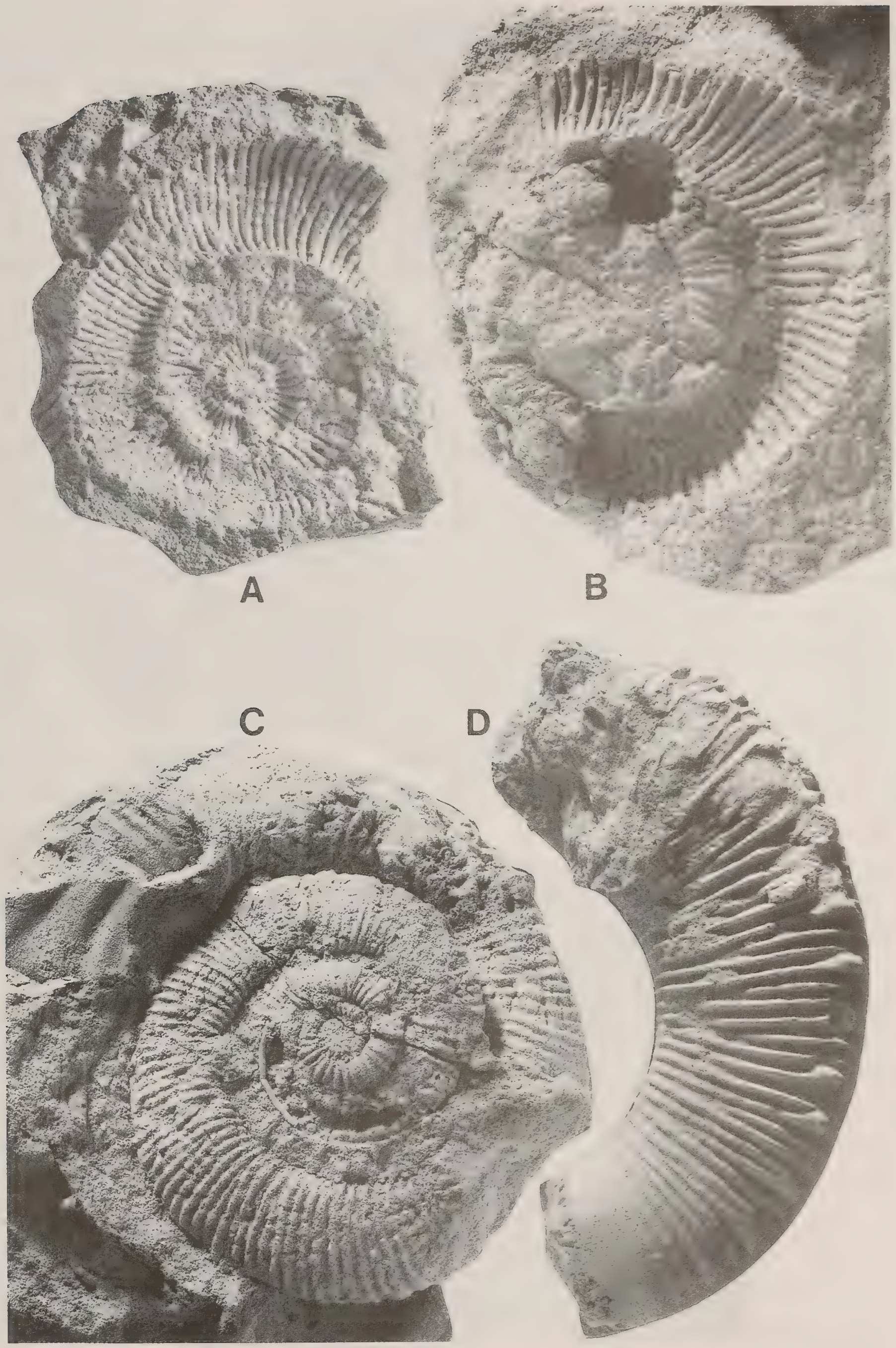

Figure 17

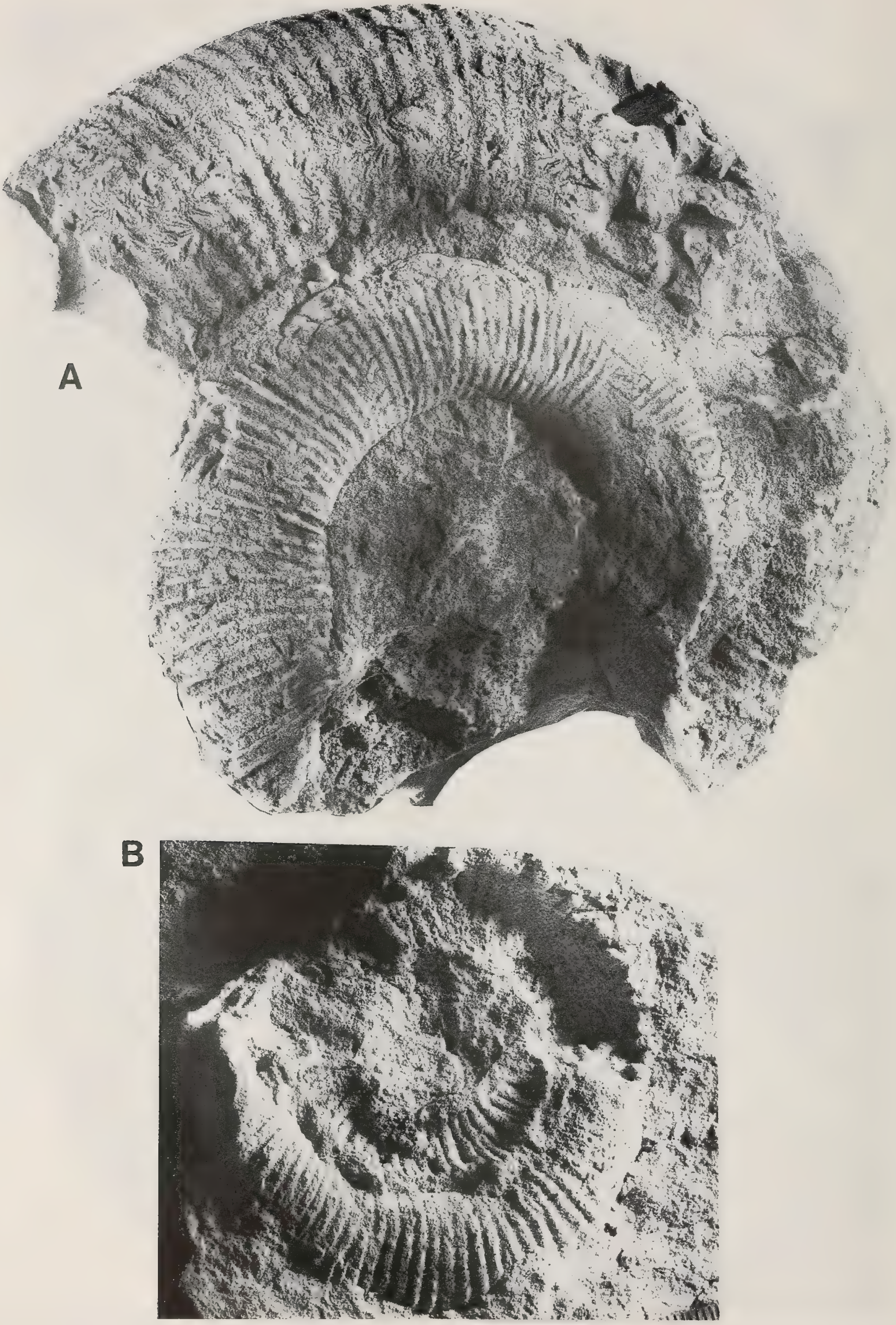

Figure 18

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). A. SAM–PCZ7907. B. SAM–PCZ10489, impression and internal mould of early ontogeny. Both from locality 113, KwaZulu, St Lucia Formation, Maastrichtian a or b. Both × 1.

spire. In contrast, in the large specimens, the body chamber may occupy up to a third of the spiral section, and the retroversal loop forms an angle of about 60 to 70 degrees with the base of the spire.

The differences in size, length of the body chamber and attitude of the retroversal loop suggest, but can not prove, that these variations are due to dimorphism. Another possible explanation is that the differences may be an adaptation to assist in orientation and buoyancy control in the adult stage.

Discussion

When Klinger (1976) first described this species, he was influenced by Wiedmann's (1962) analysis of northern German specimens of *Nostoceras (Bostrychoceras) polyplocum* (Roemer, 1841). One or possibly two of Schlüter's specimens of this species (1876, pl. 34 (figs 2–3), ?pl. 34 (figs 4–5)) with a wide apical angle and fewer whorls in the spire were referred by Wiedmann (1962: 199 footnote) to a new species, *Cirroceras depressum*. Kennedy (1986) has examined the German collections of *N. (Bostrychoceras) polyplocum* and noted the wide range of variation. It is a typically upper Campanian species, restricted mainly to Europe, but also occurs in Texas (as *Bostrychoceras secoense*) (Young, 1963: 42, pl. 3 (figs 1–5), pl. 4 (figs 4, 8), text-fig. 7s) and Mexico. The KwaZulu material occurs in the lower Maastrichtian, and is unrelated to *N. (Bostrychoceras) polyplocum* as Kennedy (1986: 97) has correctly pointed out.

We were initially inclined to refer this species to the genus *Didymoceras*. The latter, however, has distinct irregular early whorls, and is generally loosely coiled in the later stages. Consequently, we would rather place the species in the subgenus *N. (Bostrychoceras)*.

The specimens figured by Kilian & Reboul (1909, p. 15 (*pars*), pl. 5, 6 (fig. 1 only)) as *Anisoceras notabile* Whiteaves, 1879, resembles *N. (Bostrychoceras) sanctaeluciense*, but without having seen the actual material, we are uncertain whether they are the same species.

Unfortunately, the Madagascan Maastrichtian heteromorphs are mostly poorly preserved and incomplete. Klinger (1976: 67) suggested that *Nostoceras stantoni serratum* Collignon (1971: 12, pl. 644 (fig. 2383)) may be conspecific. Unfortunately this species is based on half a juvenile whorl and its relation to *N. (B). sanctaeluciense* remains unresolved.

Our study, based on the original material plus new material, clearly shows that *N.* (*N.*) *sanctaeluciense* is quite variable as far as ornament and coiling is concerned, plus the effects of probable dimorphism. A comparable wide range of variation was shown in *Didymoceras awajiense* (Yabe) by Morozumi (1985: 35, pl. 10 (figs 1–4), pl. 11 (fig. 1), pl. 12 (figs 1–2), pl. 13 (figs 1–2), pl. 14 (figs 1–2), pl. 15 (figs 1–3), text-figs 9–11) from the upper Campanian of Awaji Island, Japan. This includes specimens with a nearly planispiral phragmocone (Morozumi 1985, pl. 10 (fig. 4)), to specimens with a high turreted spire (Morozumi 1985 pl. 13 (fig. 2), pl. 14 (fig. 1)). Apart from being older (Campanian), *D. awajiense* has different ornament—on the body chamber virtually every rib is bituberculate—in contrast to the irregular tuberculation in *N. (B.) sanctaeluciense*. On account of the regular coiling of the early whorls, we suggest that *D. awajiense* should also be referred to the subgenus *N. (Bostrychoceras)*.

Nostoceras (N.) fischeri (Brunnschweiler, 1966) (*in* Henderson *et al.* 1992: 136,

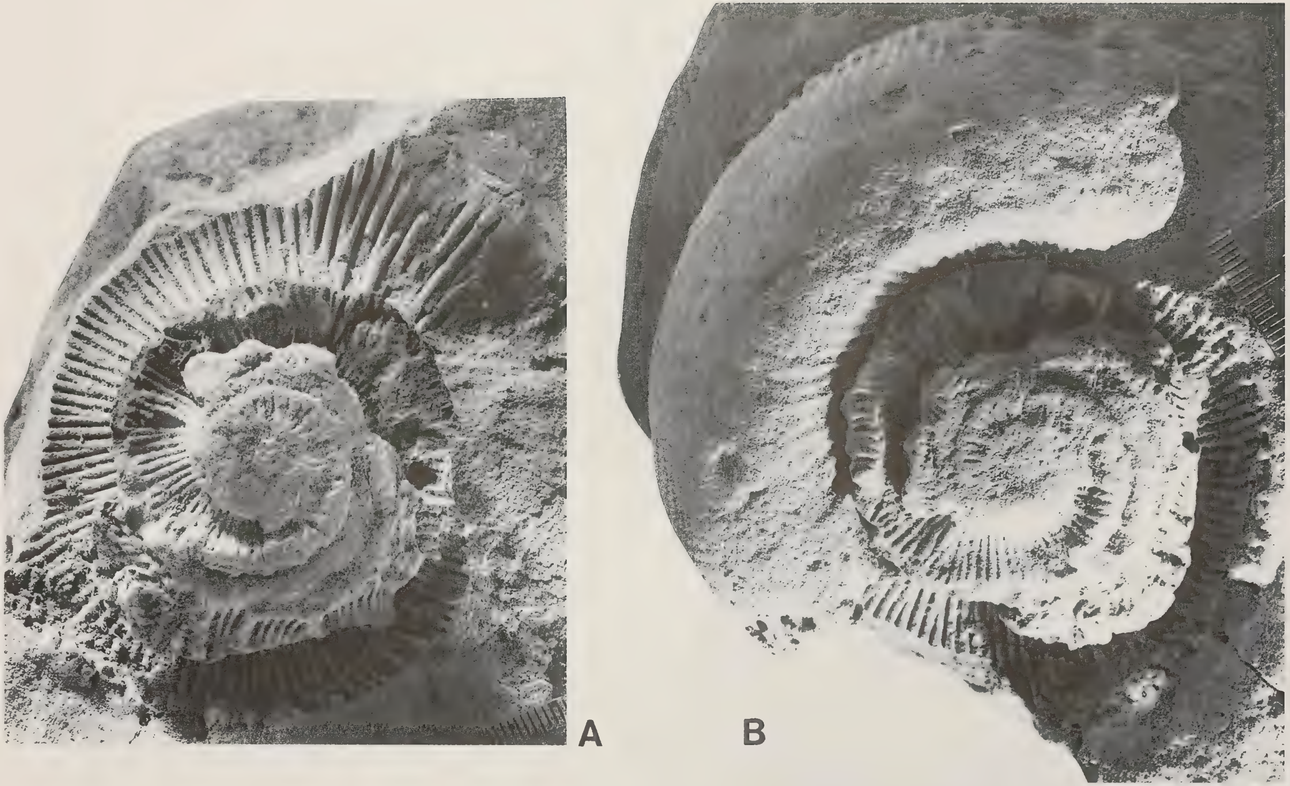

Figure 19

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). A–B. SAM–PCZ10499. The same specimen with and without the outer whorl. Again, note absence of early, irregular whorls. From locality 113, KwaZulu, St Lucia Formation, Maastrichtian a or b. Both × 1.

figs 2D–H, 3, 4A–C) from the lower Maastrichtian nodule bed of the Korojon Calcarenite of Western Australia is unfortunately represented by a few specimens only. The ornamentation of the body chamber is very similar to that of *N. (B.) sanctaeluciense*. The size difference between the largest and smallest of the body chamber hooks is comparable to that of the KwaZulu material, and Henderson *et al.* (1992: 138) have also suggested that this may be indicative of dimorphism. None of the Western Australian specimens, however, reaches such large sizes as our KwaZulu material. The largest diameter of the helicoid stage in the former is only 56 mm, compared to 85 in *N. (B.) sanctaeluciense.*

Occurrence

Lower Maastrichtian, Maastrichtian a and b of KwaZulu and possibly Seymour Island, Antarctica.

Genus *Didymoceras* Hyatt, 1894

[=*Emperoceras* Hyatt, 1894; *Didymoceratoides* Kennedy & Cobban 1993*b* (*fide* Kennedy *et al.* 2000); = ?*Cirroceras* Conrad, 1868 *nom. dub.*]

Type species

Ancyloceras nebrascense Meek & Hayden (1857: 71) by original designation of Hyatt (1894: 574).

Diagnosis

Generally large forms; initial whorls irregular, followed by loosely coiled helical section and large retroversal body chamber. Ornament generally of numerous ribs, and two rows of tubercles which may be irregularly developed.

Occurrence

Didymoceras is best known from North America (see Kennedy *et al.* 2000), but also occurs in Canada, Mexico, The Netherlands, France, Spain, Poland, Israel, Madagascar, KwaZulu, Angola and Nigeria.

Subgenus *Didymoceras (Didymoceras)* Hyatt, 1894

Type species

Ancyloceras nebrascense Meek & Hayden (1857: 71), by original designation of Hyatt (1894: 574).

Diagnosis

Early whorls irregular, sometimes hamitid, followed by loosely coiled helix and ending in retroversal body chamber hook. Ornament consists of ribs and two rows of tubercles which may be irregularly developed. Generally large.

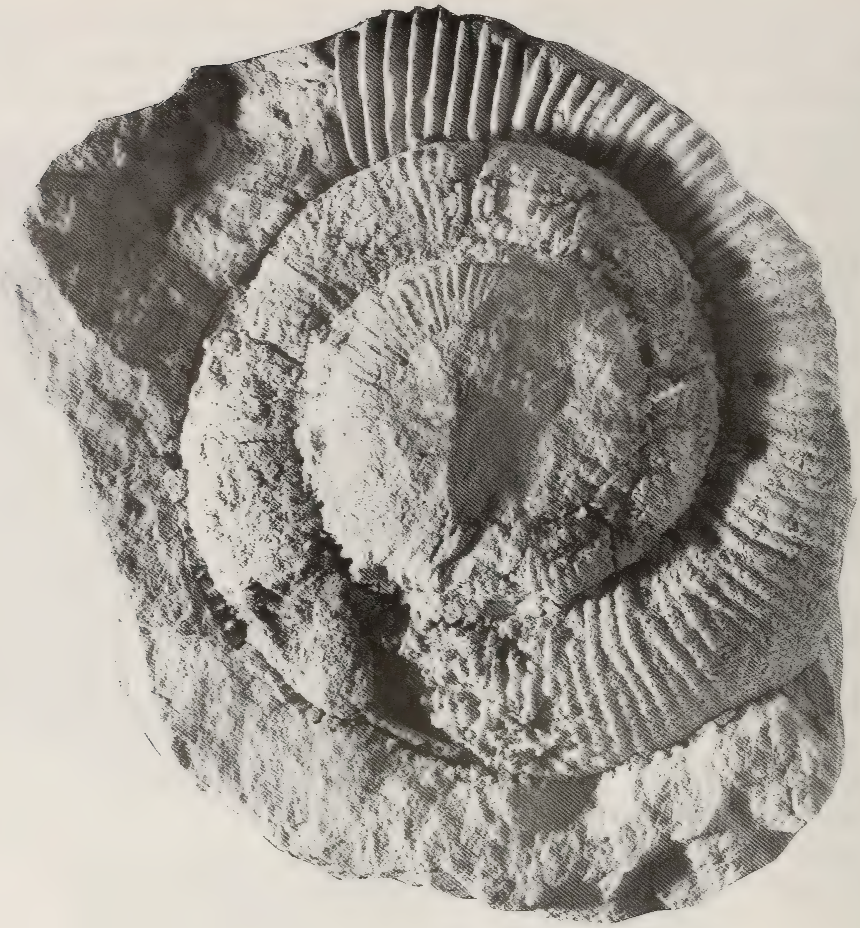

Figure 20

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). SAM–PCZ10495 from locality 113, KwaZulu, St Lucia Formation, Maastrichtian a or b. × 1.

Discussion

D. (Didymoceras) differs from *D. (Eodidymoceras)* subgen. nov. (to be described below) in being much larger, and by the distinct retroversal body chamber hook suspended below the phragmocone. It differs from *N. (Nostoceras)* by the irregular early whorls and by its generally much larger size.

Occurrence

The subgenus is best known from the Campanian and Maastrichtian of the U.S. Western Interior, but has also been recorded from the Gulf Coast region, California, the Atlantic Seaboard, Colombia, France, northern Spain, Austria, Poland, Russia, Nigeria, Angola, KwaZulu, Madagascar, ?Israel and Japan.

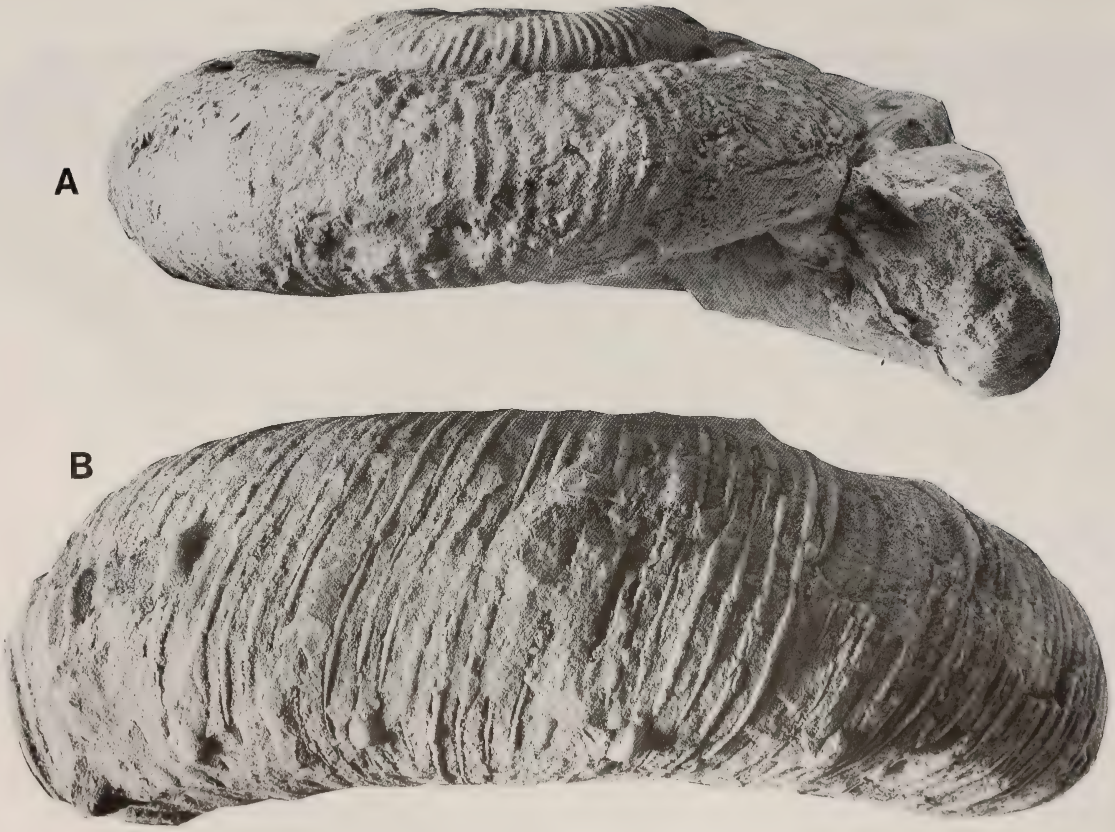

Figure 21

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). A. SAM–PCZ17341 (ex 116/7) from locality 120, KwaZulu. B. SAM–PCZ10498 (ex A2016) from locality 113, KwaZulu. Specimen with part of original ribbing preserved and the interspaces filled with sediment. Both from the St Lucia Formation, Maastrichtian a or b. Both × 1.

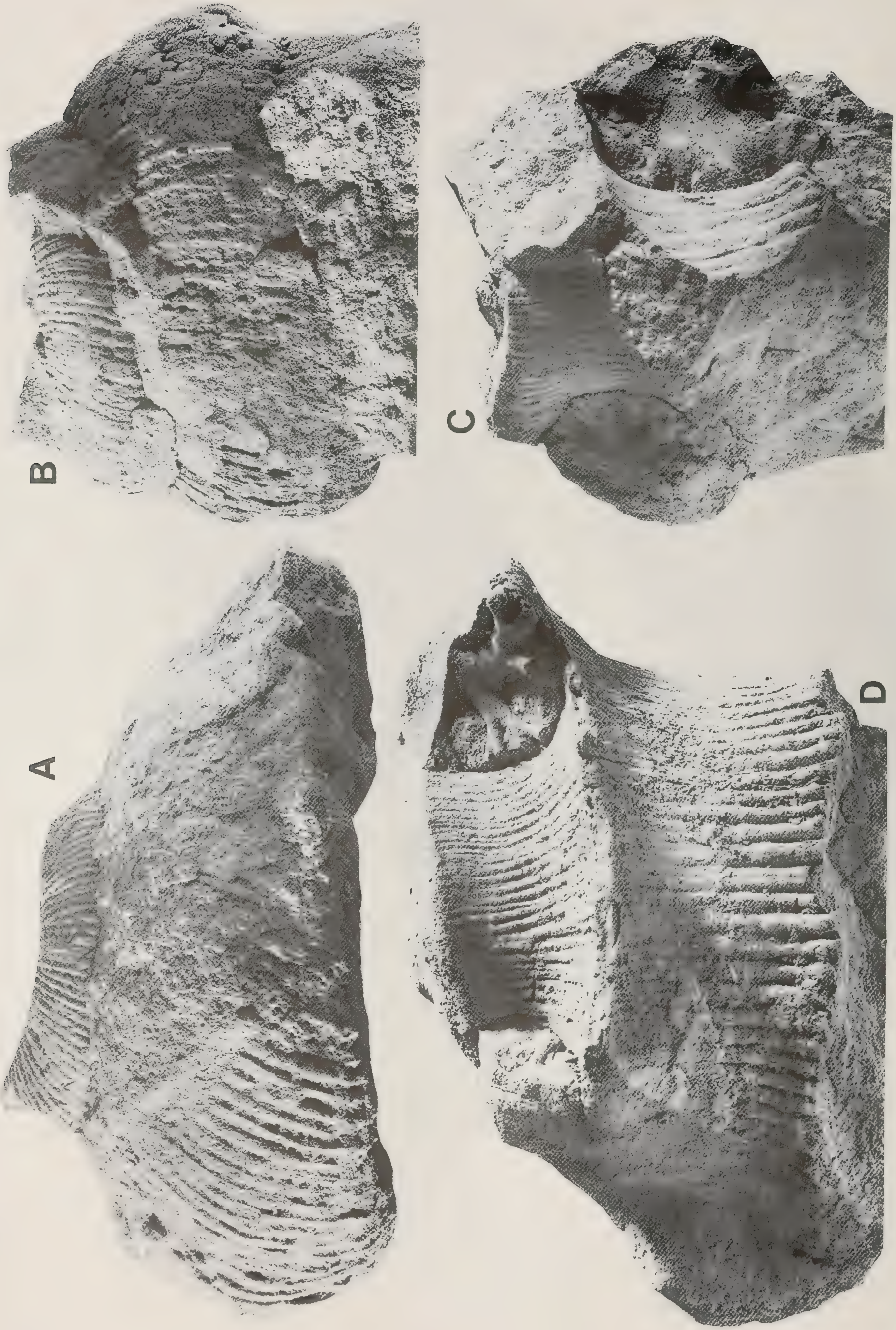

Figure 22

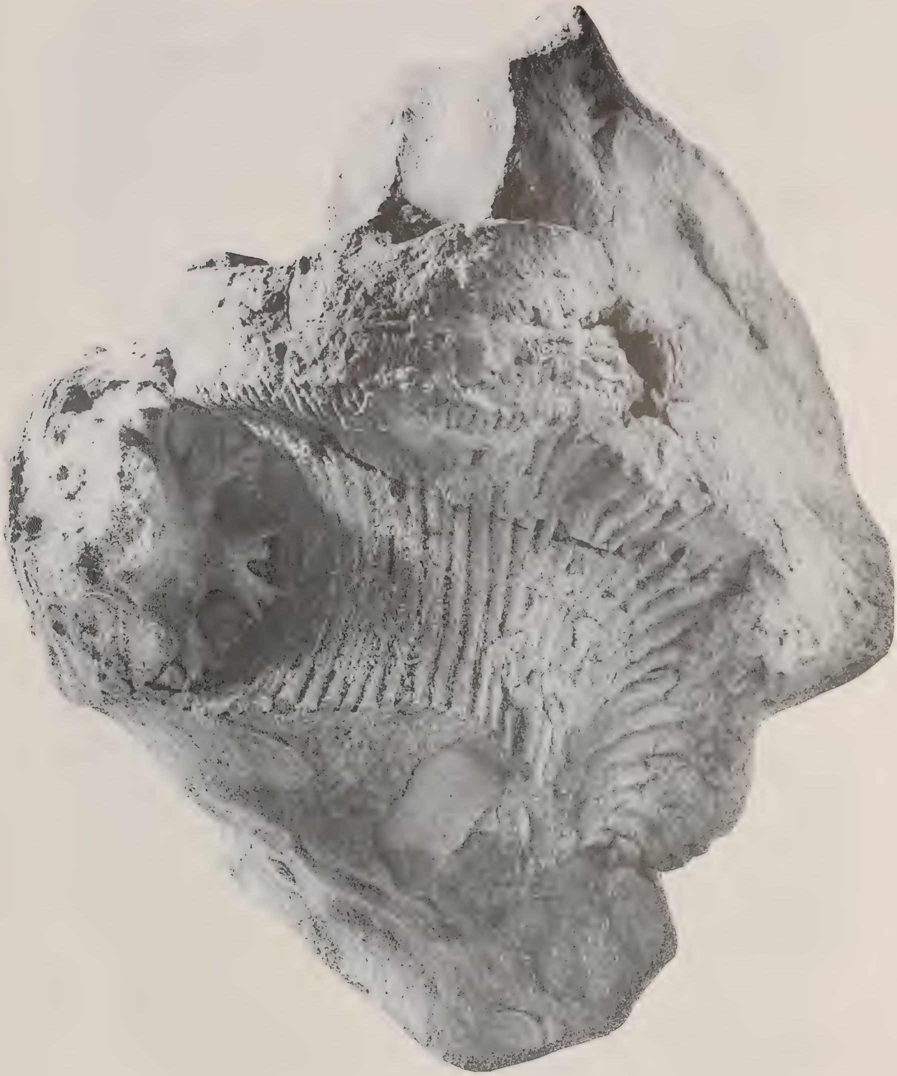

Figure 23

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). SAM–PCZ10506 from locality 125, KwaZulu, St Lucia Formation, Maastrichtian a or b. Specimen with acute apical angle on phragmocone. × 0.83.

Fig. 22. (*see facing page*). *Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). A. SAM–PCZ10494 from locality 119, KwaZulu. B. SAM–PCZ7927 imprecisely located from 'The Coves', localities 118–121, KwaZulu. C. SAM–PCZ17343 from the same locality. D. SAM–PCZ10493 from locality 125, KwaZulu. All from the St Lucia Formation, Maastrichtian a or b. All specimens with acute apical angle of phragmocone. All × 1.

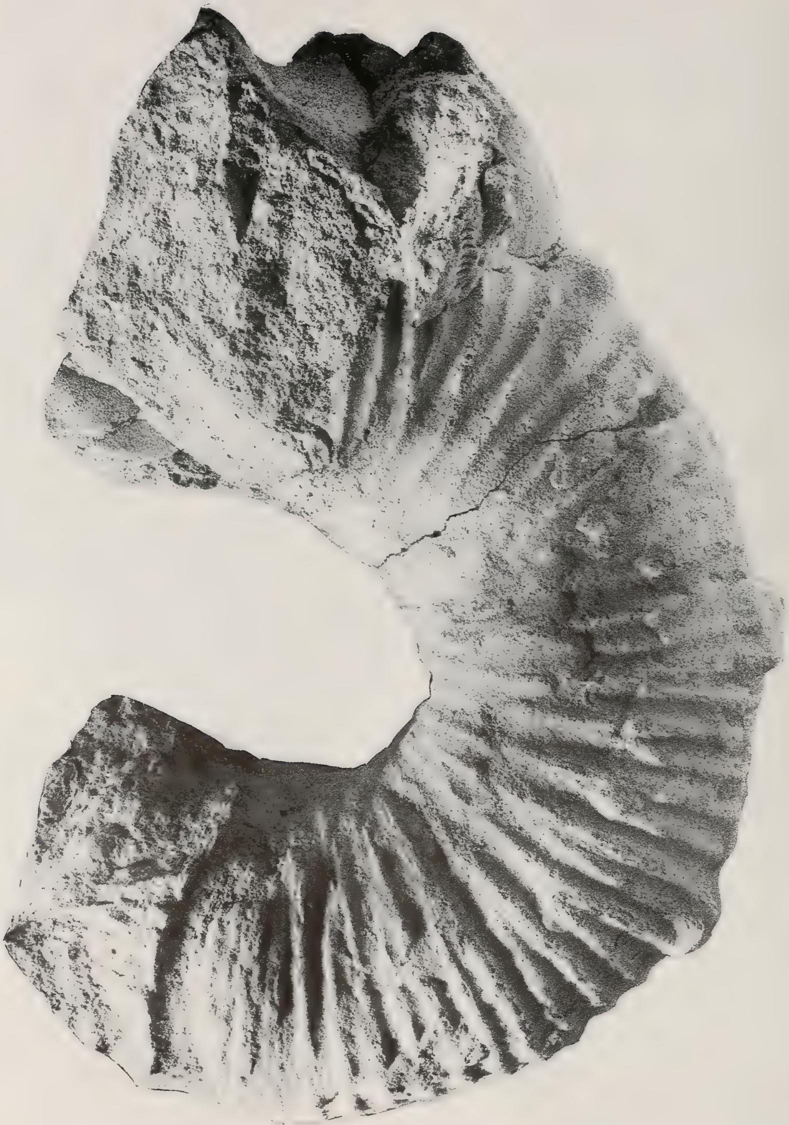

Figure 24

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). SAM–PCZ10500 from locality 125, KwaZulu, St Lucia Formation, Maastrichtian a or b. Part of recurved body chamber with preserved, constricted aperture. × 1.

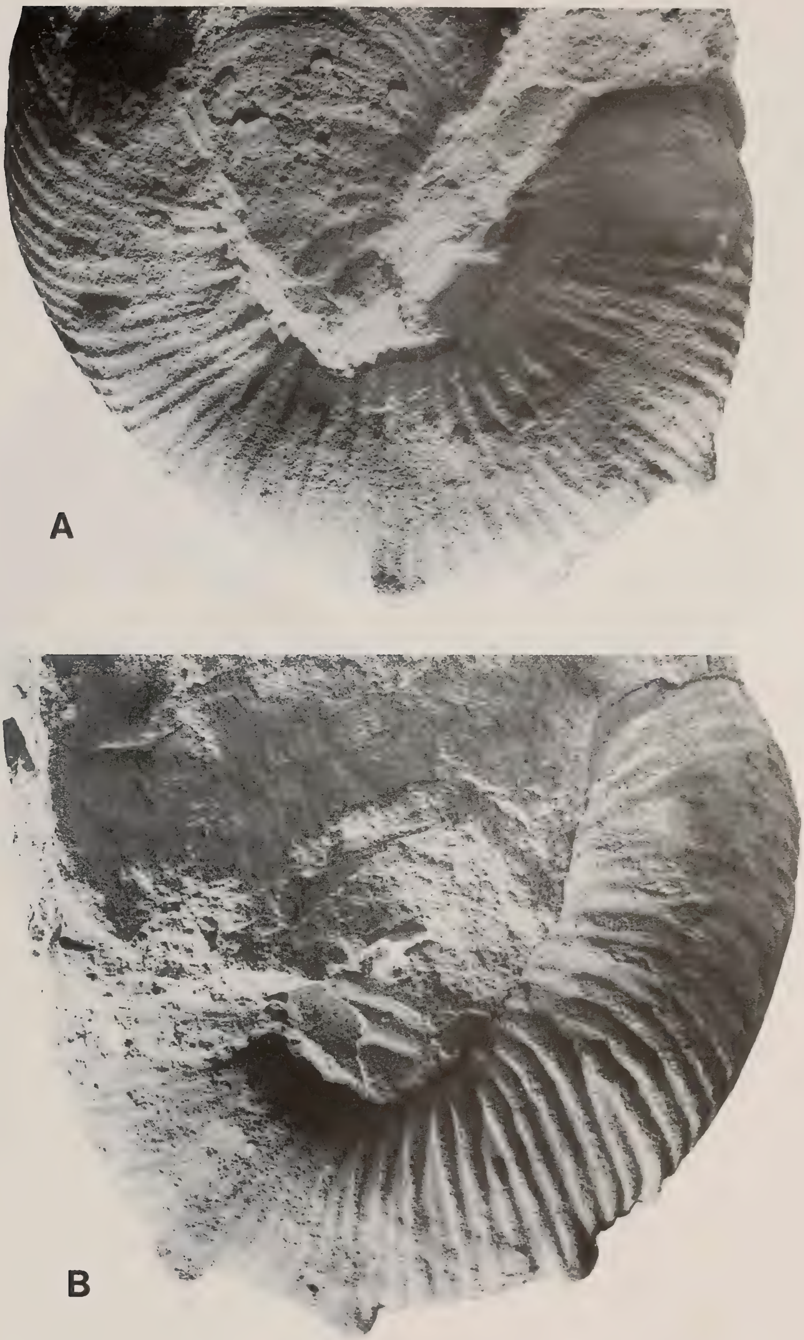

Figure 25

Nostoceras (*Bostrychoceras*) *sanctaeluciense* (Klinger, 1976). A. SAM–PCZ7902 imprecisely located from 'The Coves', localities 118–121, KwaZulu. Specimen with constricted aperture preserved. B. SAM–PCZ17344 from the same locality. Both from the St Lucia Formation, Maastrichtian a or b. Both × 1.

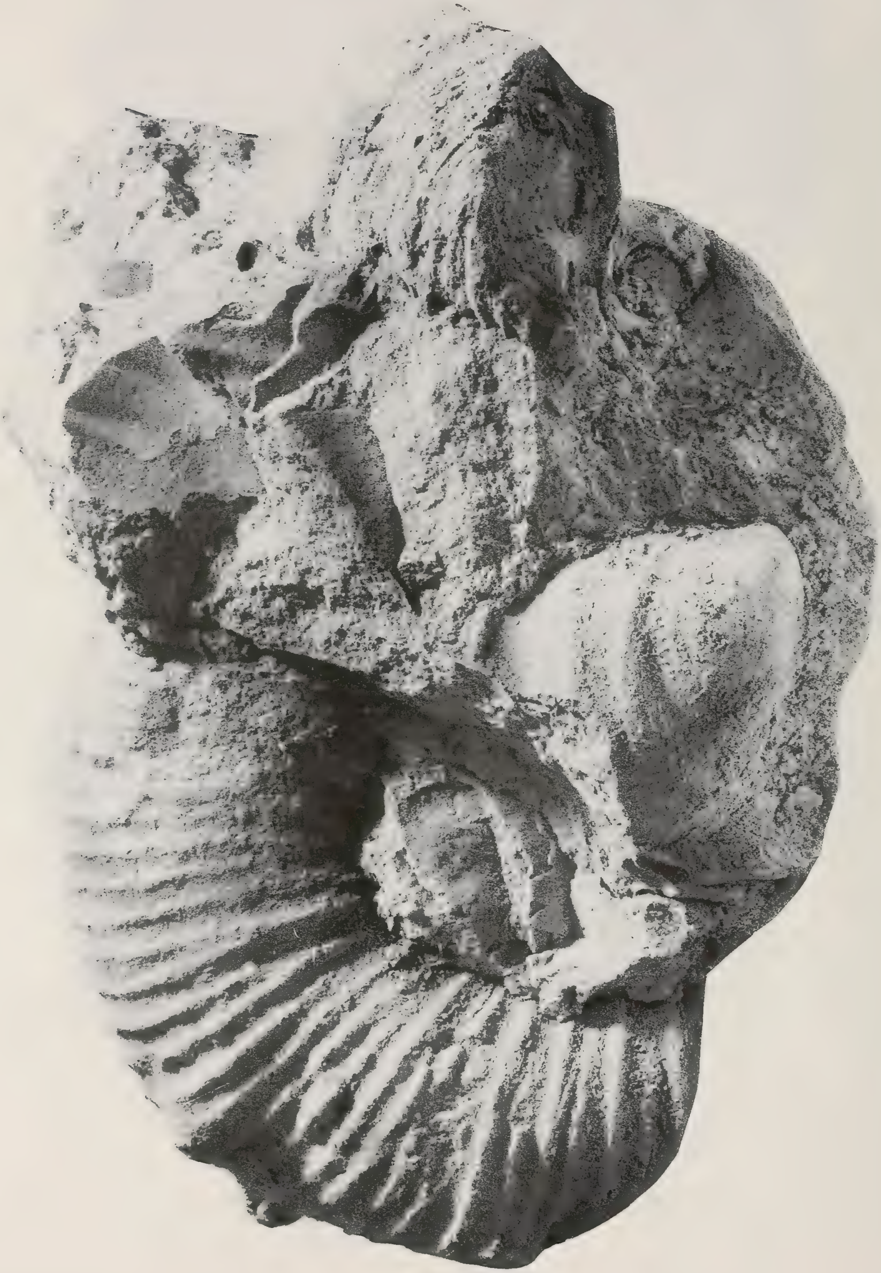

Figure 26

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). SAM–PCZ10501 from locality 125, KwaZulu, St Lucia Formation, Maastrichtian a or b. Specimen with recurved body chamber hook. × 1.

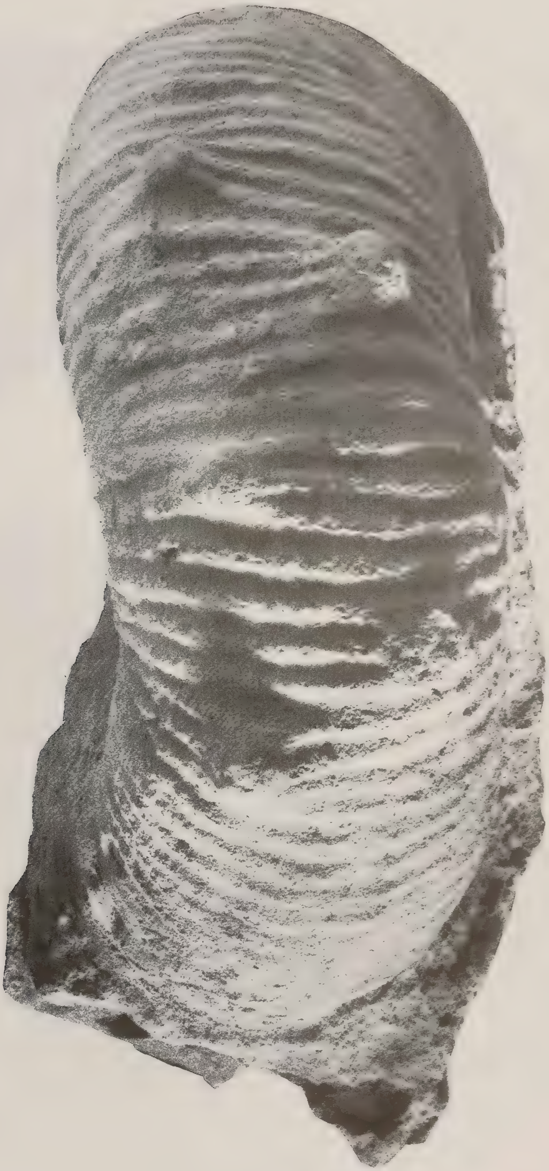

Figure 27

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). SAM–PCZ17345, imprecisely located from 'The Coves', localities 118–121, KwaZulu, St Lucia Formation, Maastrichtian a or b. Ventral view of recurved body chamber showing strong, irregular tuberculation. × 1.

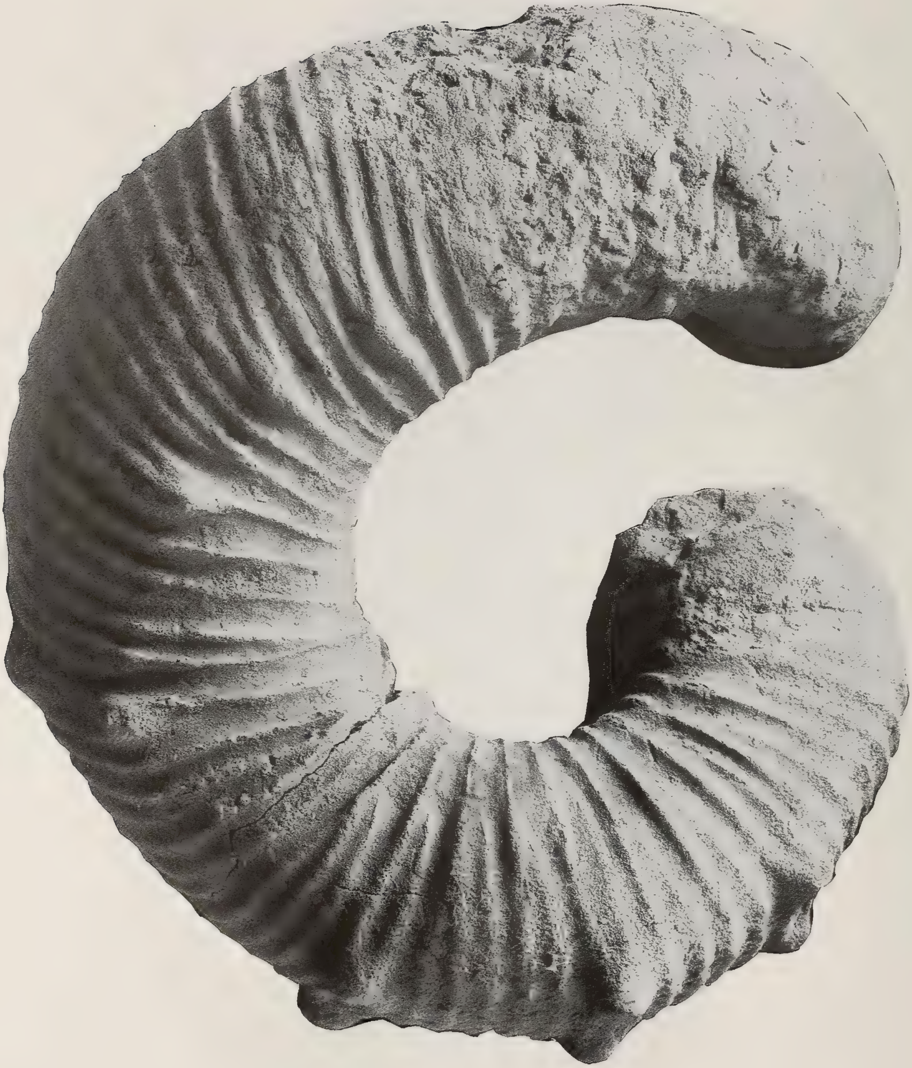

Figure 28

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). SAS–Z2251 from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b. Recurved body chamber hook showing transition from single row of tubercles to bituberculate ornamentation. × 1.

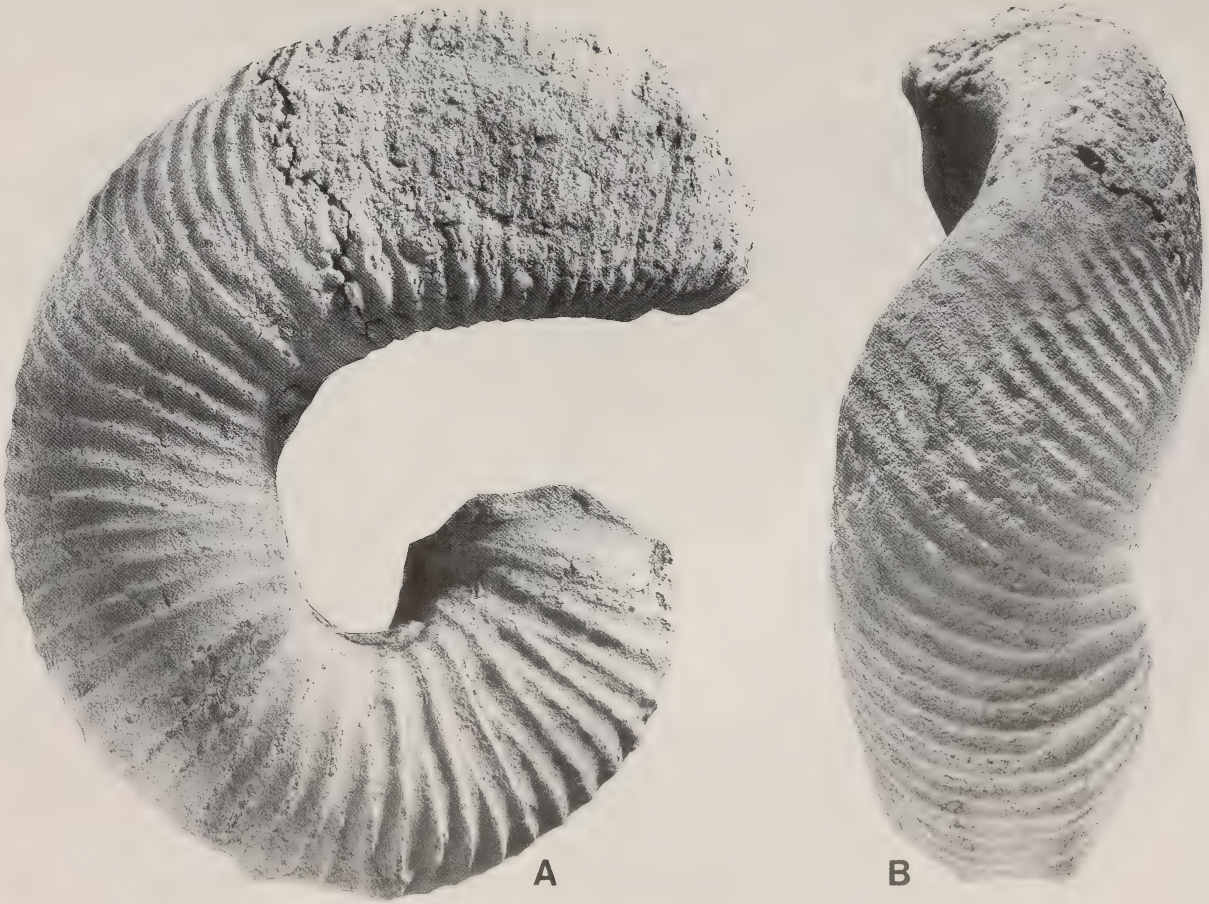

Figure 29

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). SAM–PCZ9328 from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b. Part of last helical whorl and recurved body chamber of adult microconch. × 1.

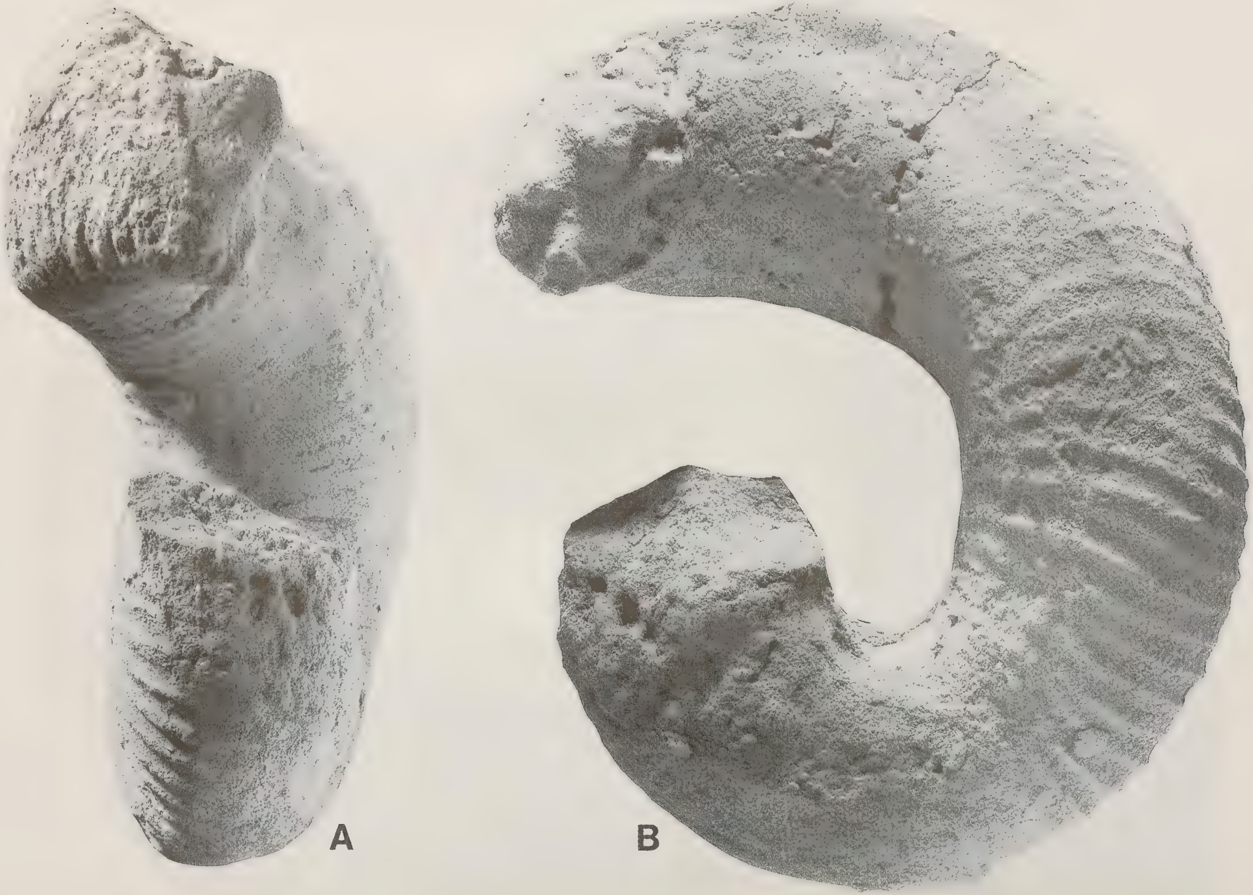

Figure 30

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). SAM–PCZ9328 from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b. Microconch with recurved body chamber suspended at right angles below base of helical phragmocone. × 1.

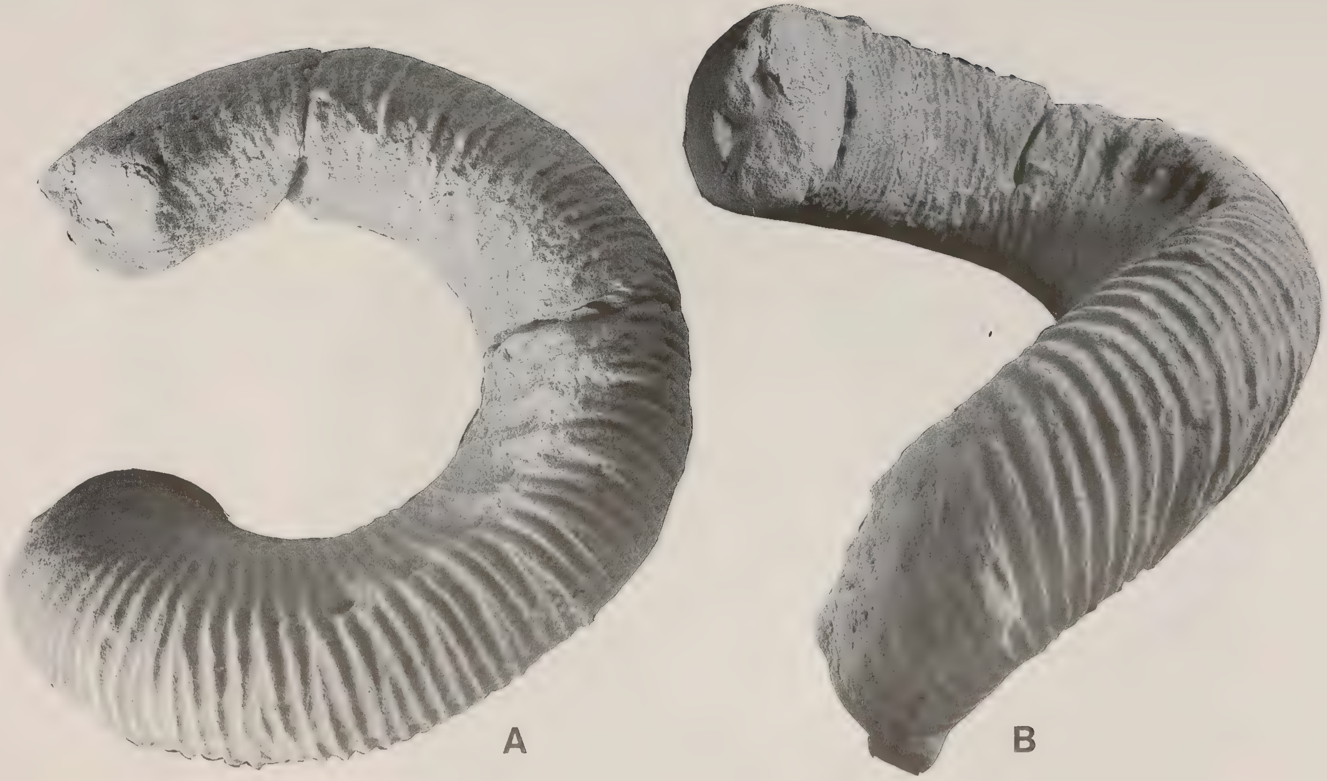

Figure 31

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). SAM–PCZ17346 imprecisely located from 'The Coves', localities 118–121, KwaZulu, St Lucia Formation, Maastrichtian a or b. Macroconch with last part of helical section and recurved body chamber hook preserved. Note impression of ventral tubercles on inner edge of last part of helical section. × 0.5.

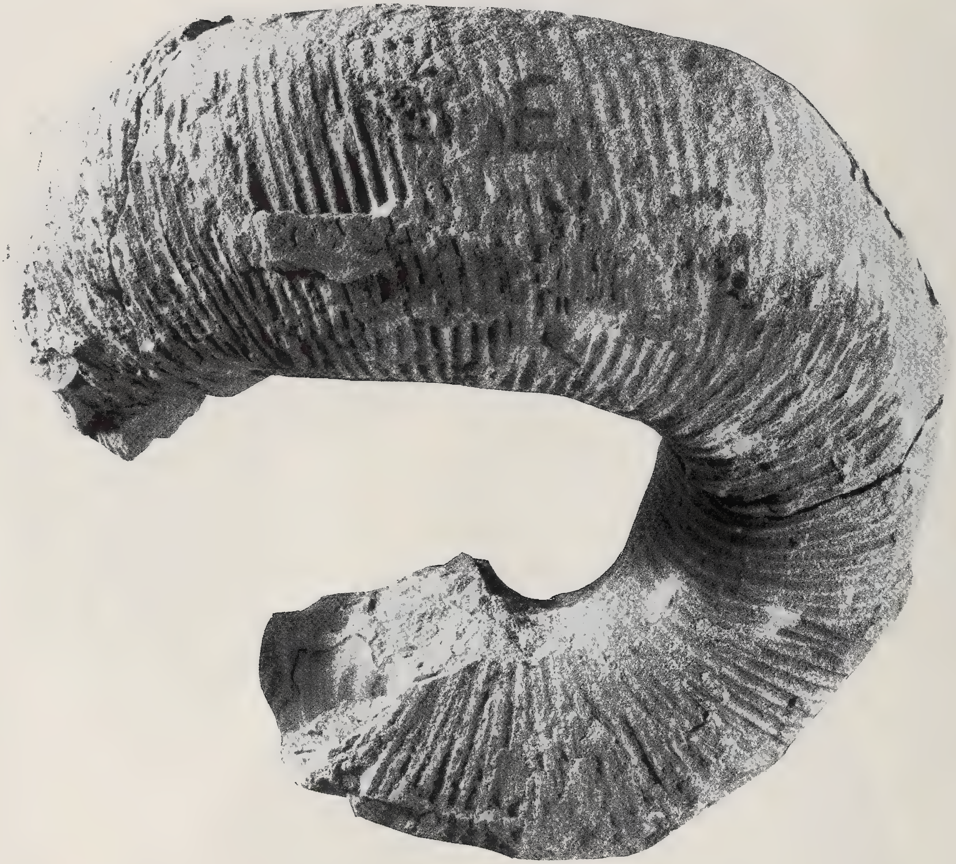

Figure 32

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). SAM–PCZ9431 (ex 113E) from bed E at locality 113, KwaZulu, St Lucia Formation, Maastrichtian b. Macroconch, part of last helical whorl and recurved body chamber. × 0.58.

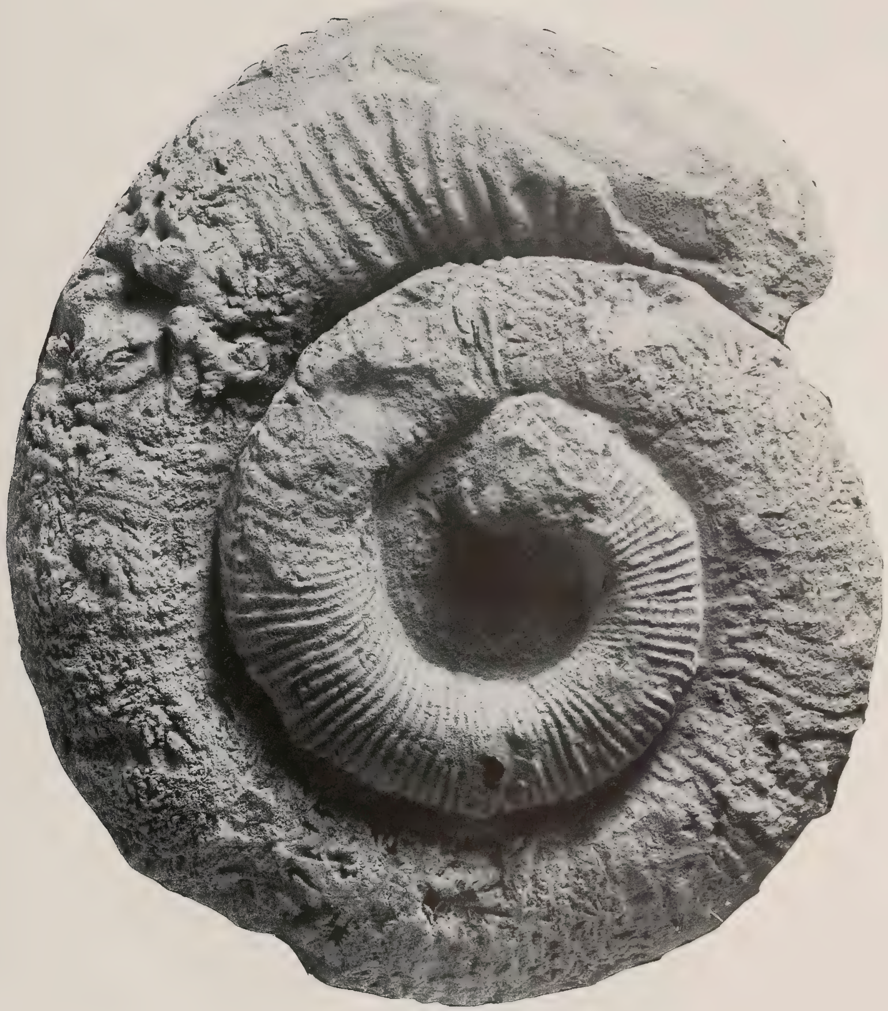

Figure 33

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). SAM–PCZ17341 (ex SAS–H116/7 from locality 120, KwaZulu, St Lucia Formation, Maastrichtian b. × 1.

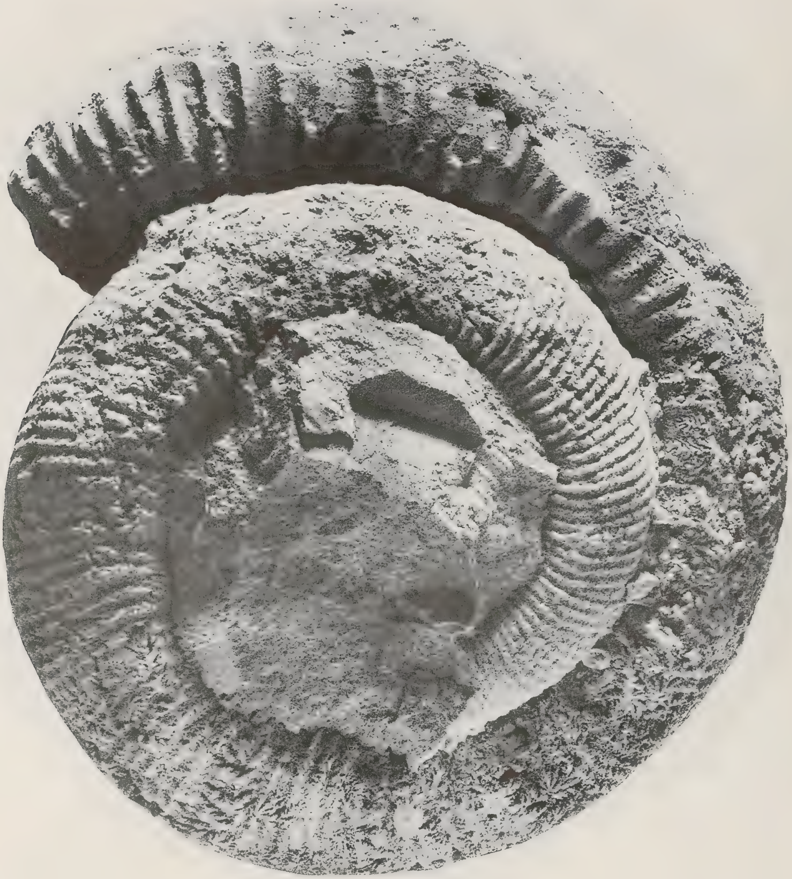

Figure 34

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). SAM–PCZ10504 imprecisely located from 'The Coves', localities 118–121, KwaZulu, St Lucia Formation, Maastrichtian a or b. × 0.7.

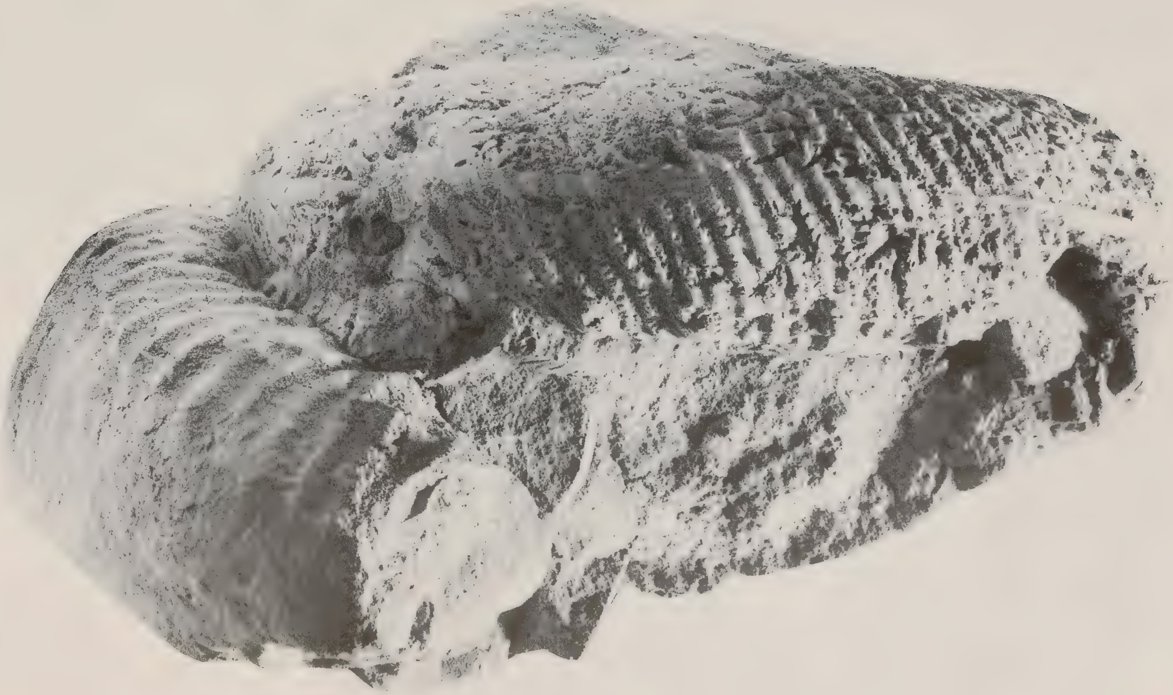

Figure 35

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). SAM–PCZ10504 imprecisely located from 'The Coves', localities 118–121, KwaZulu, St Lucia Formation, Maastrichtian a or b. × 1.

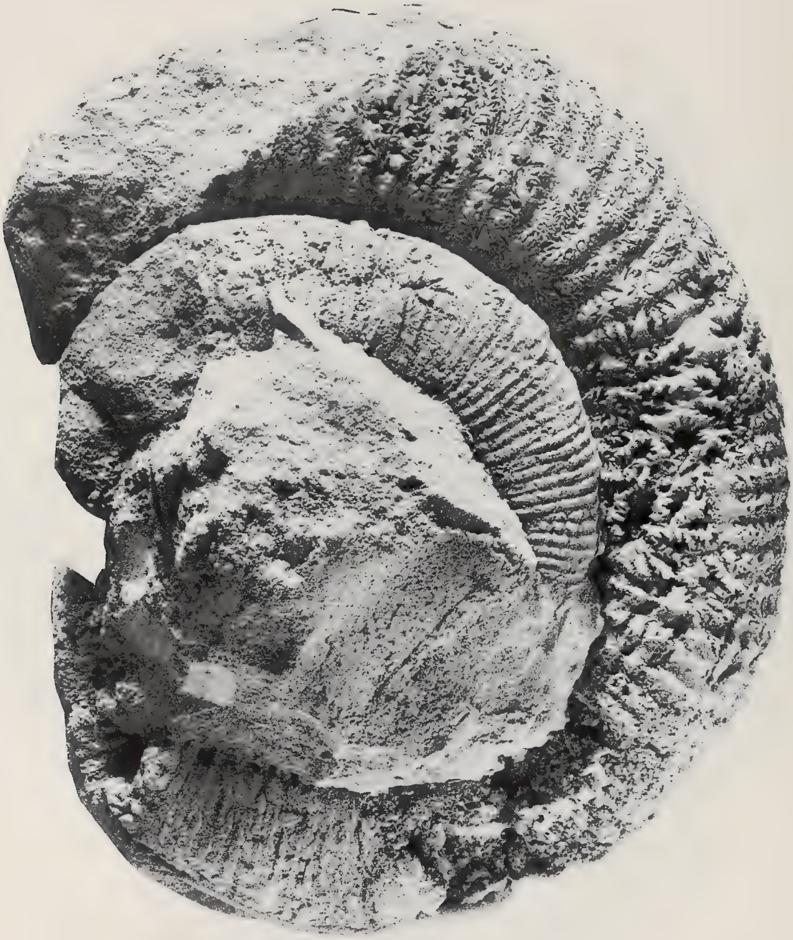

Figure 36

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). SAM–PCZ10507 from locality 125, KwaZulu, St Lucia Formation, Maastrichtian a or b. × 1.

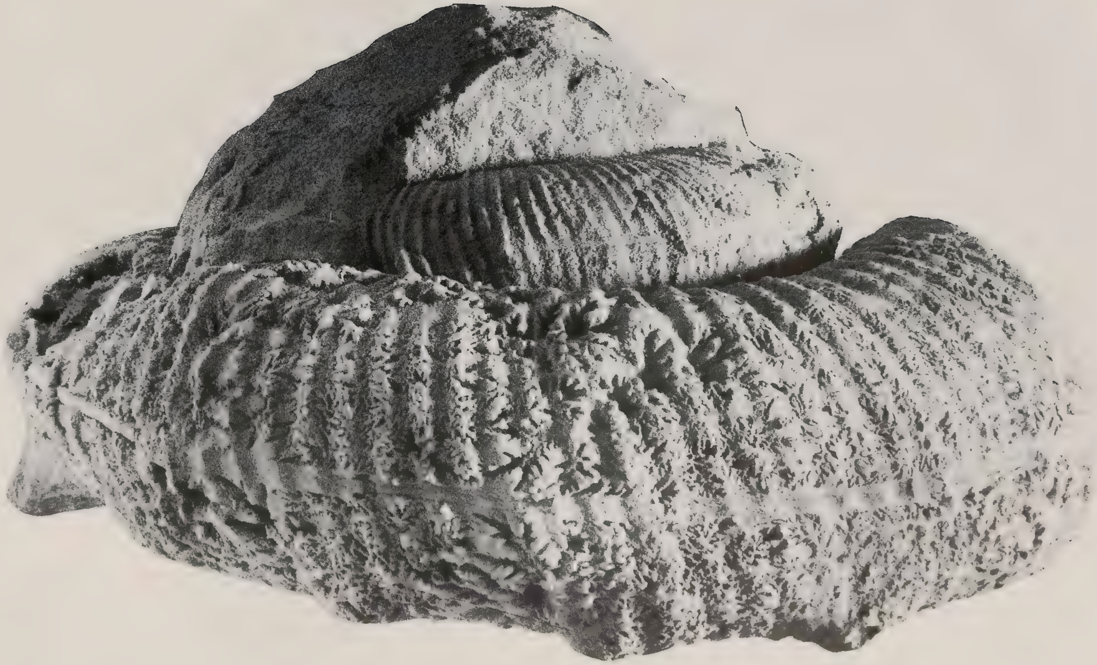

Figure 37

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). SAM–PCZ10507 from locality 125, KwaZulu, St Lucia Formation, Maastrichtian a or b. × 1.

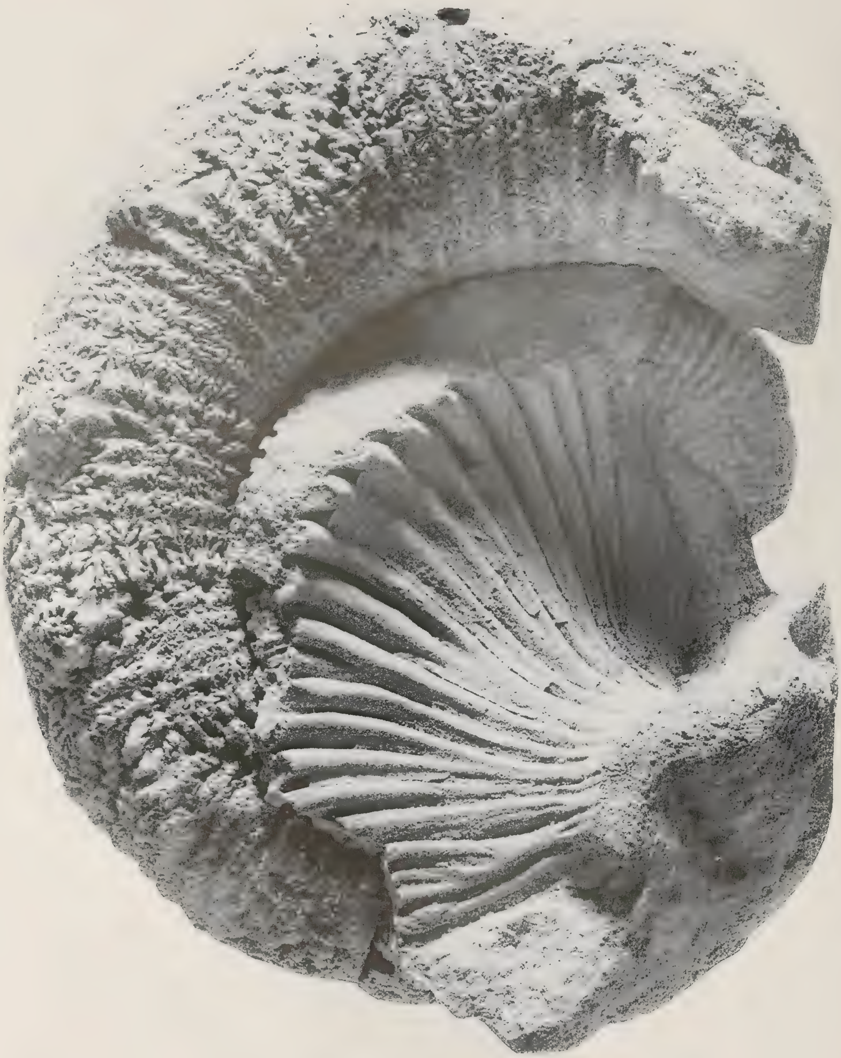

Figure 38

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). SAM–PCZ10507 from locality 125, KwaZulu, St Lucia Formation, Maastrichtian a or b. View of venter of last phragmocone whorl and impression of recurved body chamber. × 1.

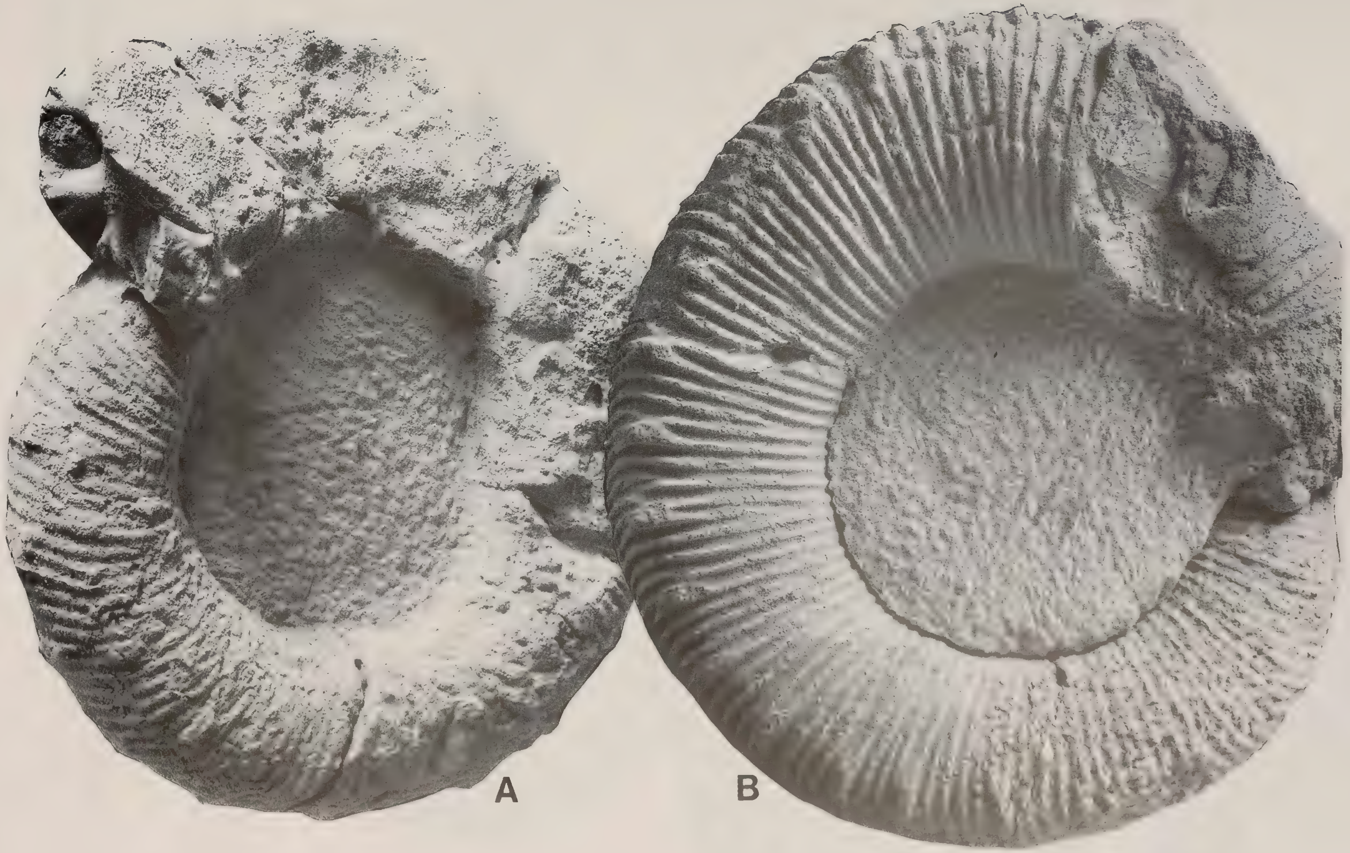

Figure 39

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). A. SAM–PCZ17349 (ex SAS–H115/15). B. SAM–PCZ17350 (ex SAS–H115/13). Both from locality 120, KwaZulu, St Lucia Formation, Maastrichtian a or b. Ventral view of specimens to show appearance of abapical tubercles. Both × 1.

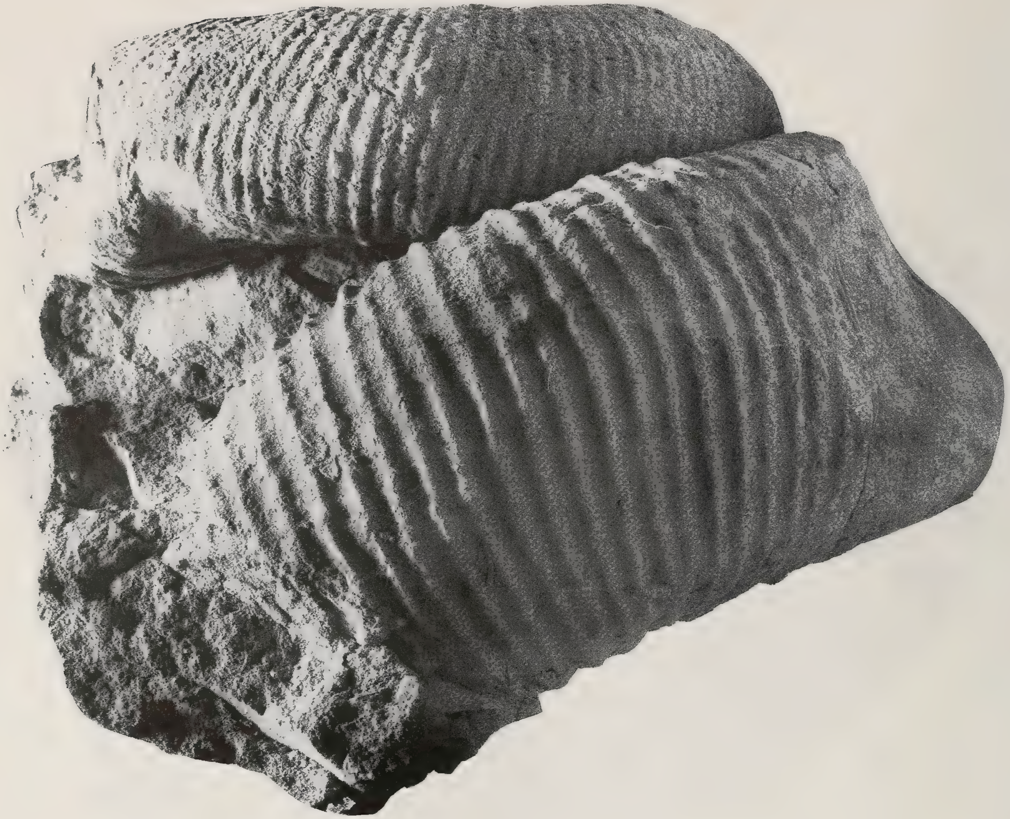

Figure 40

Nostoceras (Bostrychoceras) sanctaeluciense (Klinger, 1976). SAM–PCZ10504 imprecisely located from 'The Coves', localities 118–121, KwaZulu, St Lucia Formation, Maastrichtian a or b. × 1.

Didymoceras (D.) australis sp. nov.

Figs 41–44, 50B–C

Type

Holotype is SAM–PCZ17351 from locality 109C, western part of Nibela Peninsula, KwaZulu, St Lucia Formation, Campanian III.

Material

SAM–PCZ7576 and SAM–PCZ9332, both from the same locality as the holotype. SAM–PCZ18749, SAM–PCZ18748, NMB–D1490, all presumably from the same locality.

Etymology

Named for its occurrence in the southern hemisphere.

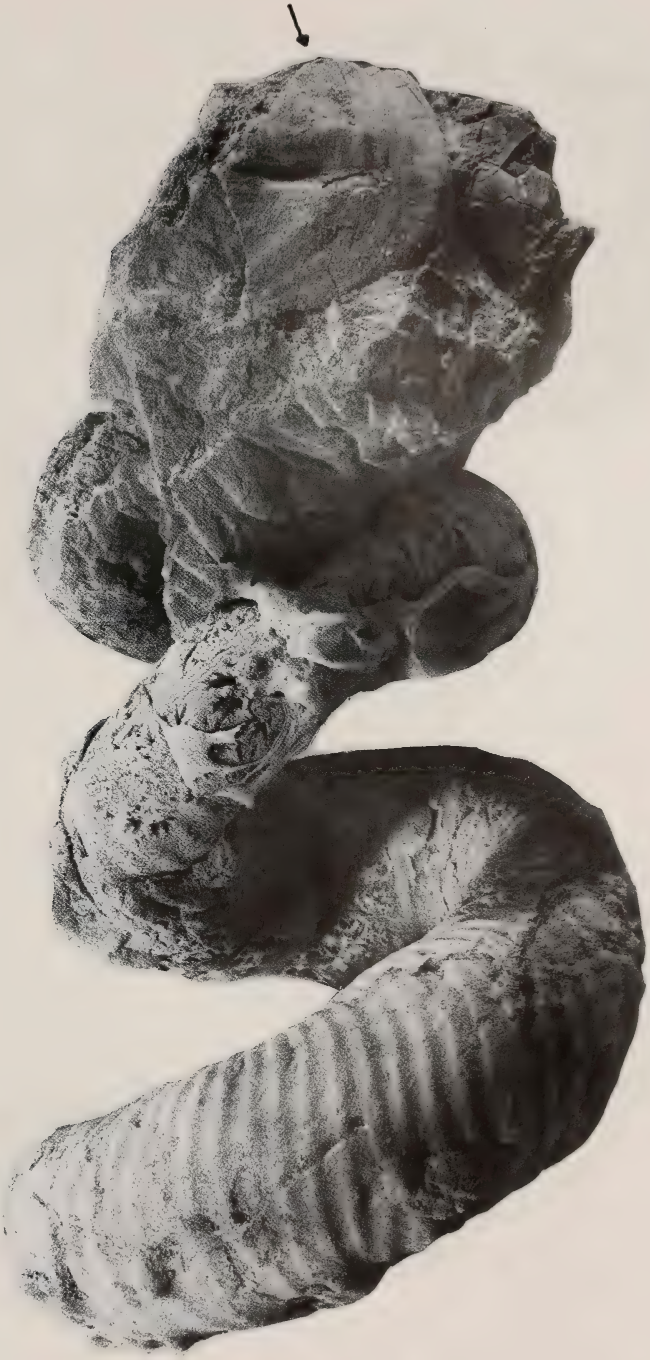

Figure 41

Didymoceras (Didymoceras) australis sp. nov. The holotype, SAM–PCZ17351 from locality 109c, KwaZulu, St Lucia Formation, Campanian III. With part of what appears to be an anaptychus (arrow). × 0.8

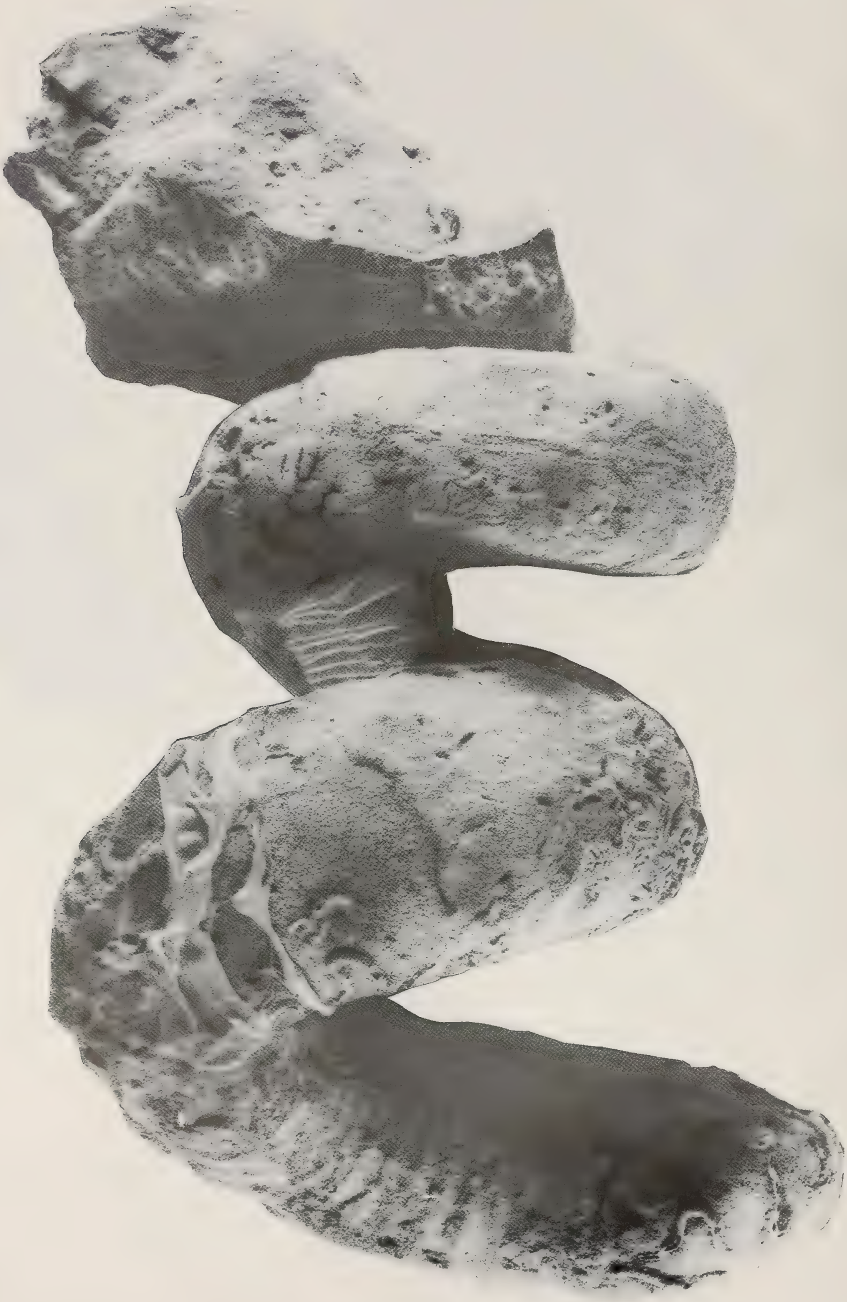

Figure 42

Didymoceras (Didymoceras) australis sp. nov. The holotype, SAM–PCZ17351 from locality 109c, KwaZulu, St Lucia Formation, Campanian III. × 0.8.

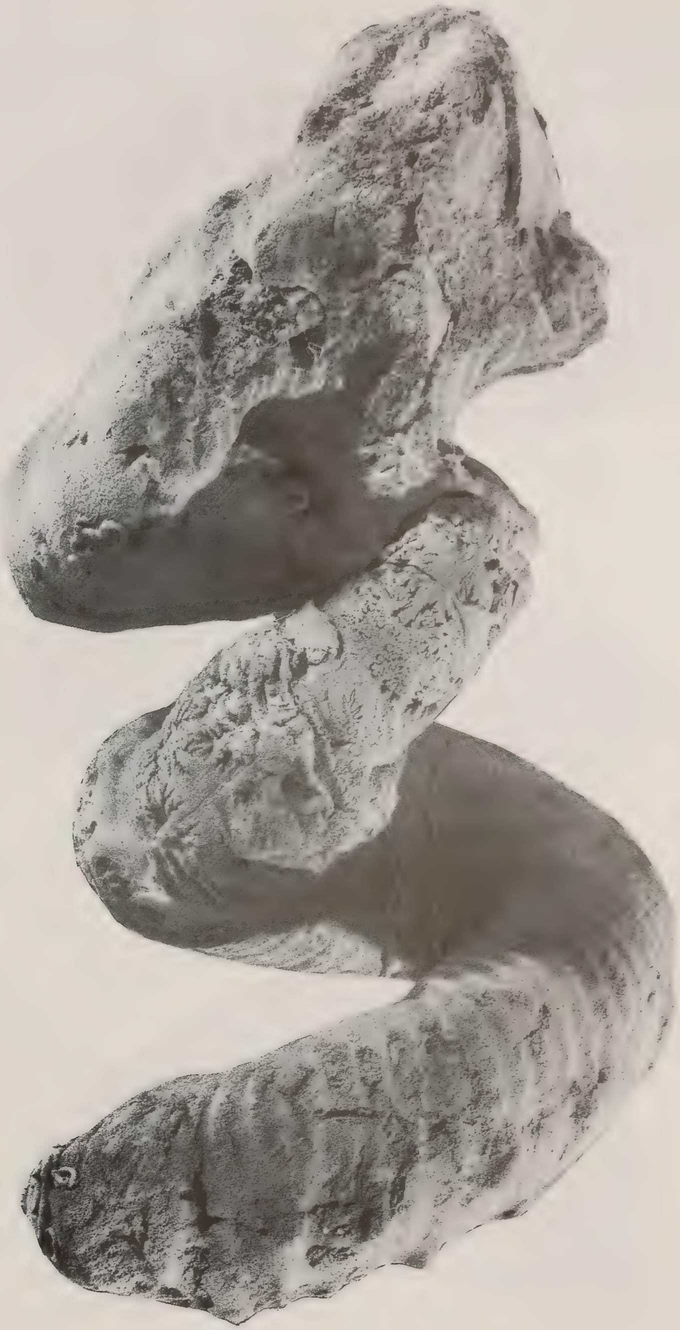

Figure 43

Didymoceras (Didymoceras) australis sp. nov. The holotype, SAM–PCZ17351 from locality 109c, KwaZulu, St Lucia Formation, Campanian III. × 0.8.

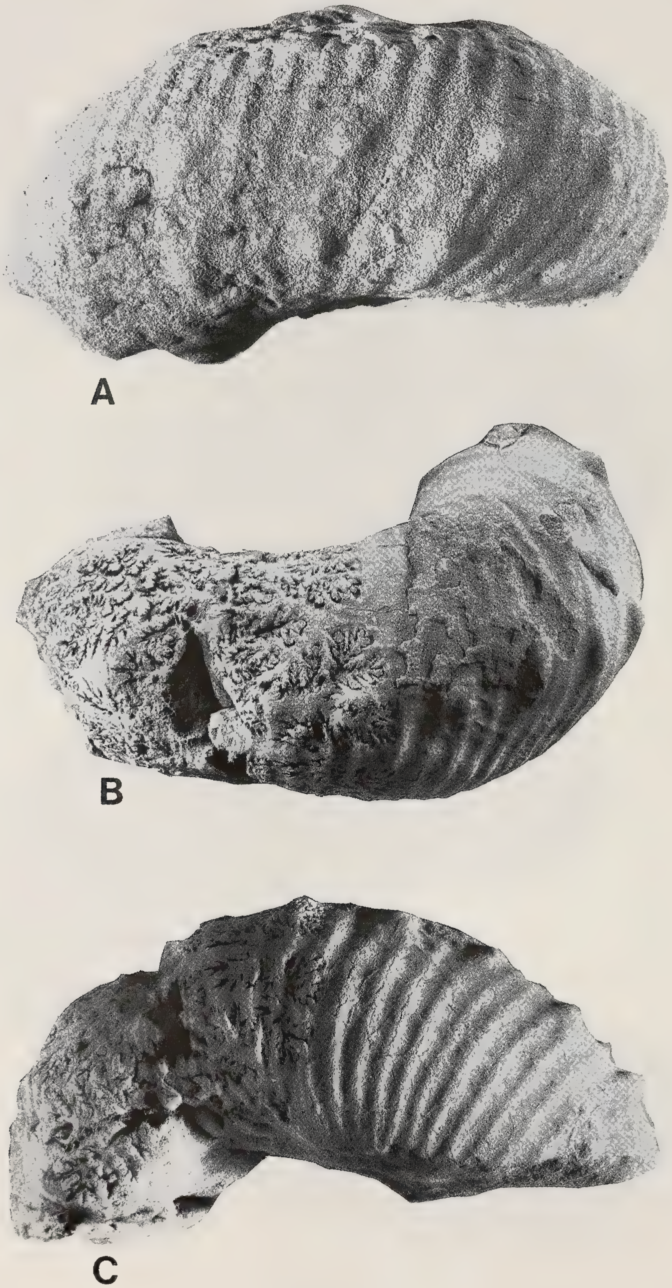

Figure 44

Didymoceras (Didymoceras) australis sp. nov. SAM–PCZ7576 from locality 109c, KwaZulu, St Lucia Formation, Campanian III. × 1.

Description

The holotype SAM–PCZ17351 consists of at least two helically coiled whorls of which the last half a whorl is non-septate. The paratypes all consist of less than half a whorl.

Ornament on the phragmocone consists of low, dense ribbing and two large, but weakly developed and irregularly spaced rows of tubercles—one just below the siphuncle and the other near the abapical part of the whorl. Ornament becomes stronger on the body chamber and sharp-crested ribs are conspicuous, but the tubercles are still poorly developed.

The suture line is extremely complex. A structure resembling an anaptychus is situated between the early whorls of the holotype (Fig. 41, arrow). We do not know if this structure belongs to the present species or to the associated ammonite fauna.

Discussion

Size, coiling and ornament clearly distinguish this specimen from all other known KwaZulu nostoceratids.

The closest match we can find with our material is *D. (D.) nebrascense* from the upper Campanian of the U.S. Western Interior. The reconstruction in Scott & Cobban (1965) (see also Gill & Cobban 1973, fig. 5a; Kennedy *et al.* 2000: 7, figs 3–4, 6–7, 8c, d, 9–13, 62)) shows loose, helical coils and poorly developed tuberculation on the phragmocone, compared to the stronger ornament in the younger *D. (D.) stephensoni* and *D. (D.) cheyennense.*

Occurrence

Campanian III of KwaZulu.

Didymoceras (Didymoceras) sp.

Fig. 45

Material

SAM–PCZ7638 from locality 109C, the western part of Nibela Peninsula, KwaZulu, St Lucia Formation, Campanian III.

Description and discussion

A single specimen differs from *Didymoceras (D.) australis* in being much larger and still septate at a diameter of *c.* 50 mm, and in having tighter coiling. This specimen may connect with the largest fragment of *D. (D.) australis*, SAM–PCZ7576 in having a similar mode of ornamentation. It is possible that the differences in size are due to dimorphism, but with the limited material available, it is impossible to say with certainty.

Occurrence

Campanian III of KwaZulu.

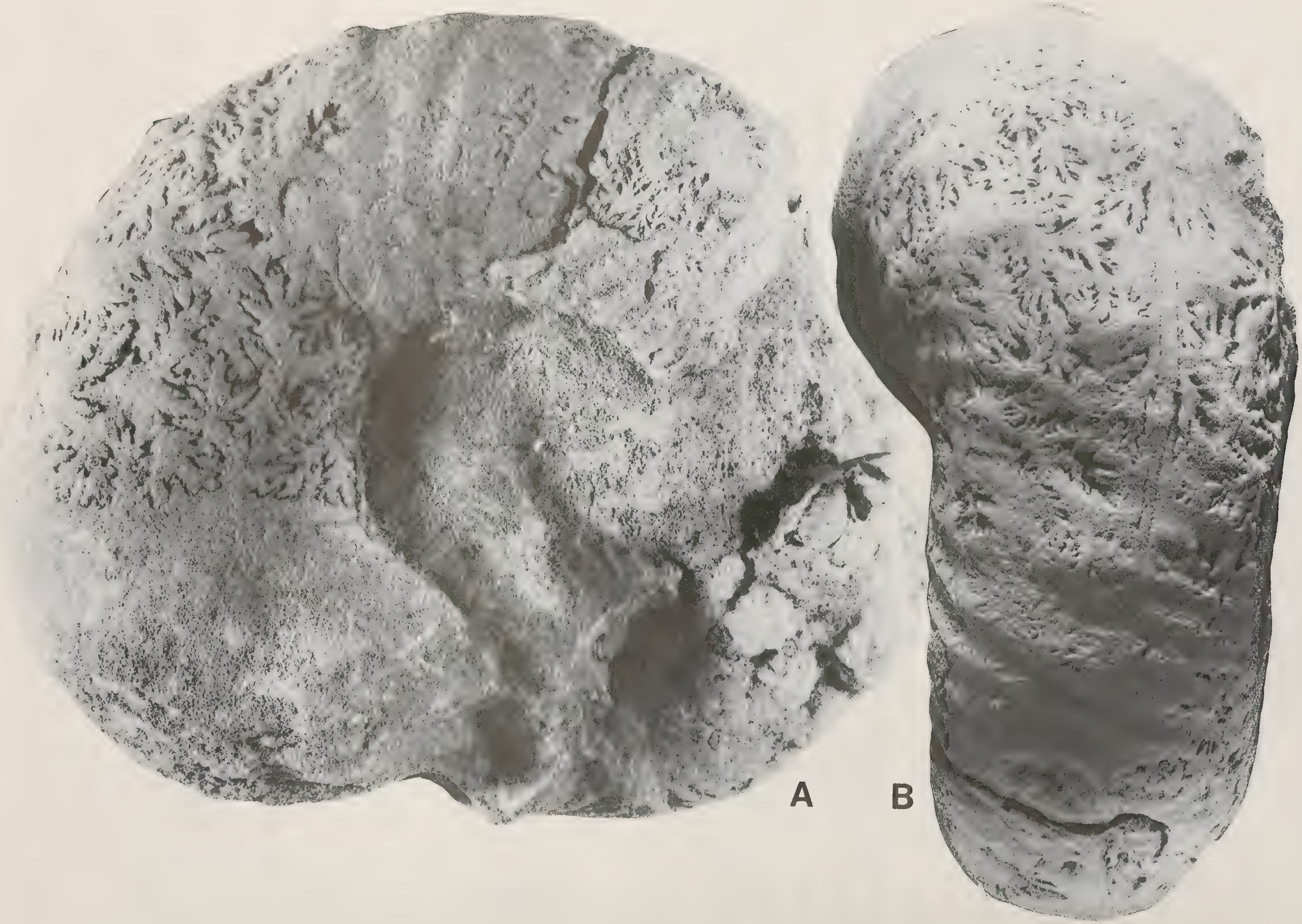

Figure 45

Didymoceras (Didymoceras) sp. SAM–PCZ7638 from locality 109c, KwaZulu, St Lucia Formation, Campanian III. × 1.

Didymoceras (Didymoceras?) africanum sp. nov.

Figs 46, 47A–C

Type

Holotype by monotypy is SAM–PCZ7637 from locality 109C, western part of Nibela Peninsula, KwaZulu, St Lucia Formation, Campanian III.

Etymology

Named after its geographic occurrence.

Description

The holotype consists of a large, virtually planispirally coiled half of a whorl, part of an earlier whorl impressed in the matrix of the former on the inner adapical edge, and a fragment of an even earlier whorl, found loose in the same block of matrix.

Coiling in the spiral section of the shell is extremely loose, forming a low spire with a very wide umbilicus. Ornament consists of numerous, sharp-crested ribs. These are weak on the inner (dorsal) side of the whorl, and strongest on the adapical and abapical parts of the whorls. Two rows of tubercles are situated on the ventral (siphonal) part of the whorls. The first is slightly adapical of the midline and the second just above the abapical edge. These are connected adapically and abapically by irregularly looped or single ribs; some of the ribs are not connected to tubercles at all. In the area between the tubercles the ribs weaken and form loops or are connected in a zig-zag pattern (Fig. 47B–C).

Discussion

The asymmetric position of the tubercles on the venter (flanks) and the impression of a smaller whorl above the largest suggest that this is indeed a very low-spired species of *Didymoceras*, and not, perhaps, a representative of *Exiteloceras*, *Lewyites*, or *Neancyloceras*. *Exiteloceras jenneyi camacki* Kennedy *et al.* (2000: 62, figs 44D, 49–50) is superficially similar to the present species as far as the large size is concerned, but differs in being planispirally coiled.

The low coiling and consistent, strongly bituberculate ornament easily distinguishes *D. (D.?) africanum* from the coeval *D. (D.) australis*, as well as from the younger *N. (Bostrychoceras) sanctaeluciense*. Some specimens of *N. (B.) awajiense* (Yabe) figured by Morozumi (e.g. 1985, pl. 10 (fig. 4a–c)) have a similar very low apical angle, but again the coarser ribbing and regular bituberculation distinguish *D. (D.?) africanum* from this Japanese species.

Occurrence

Campanian III of KwaZulu.

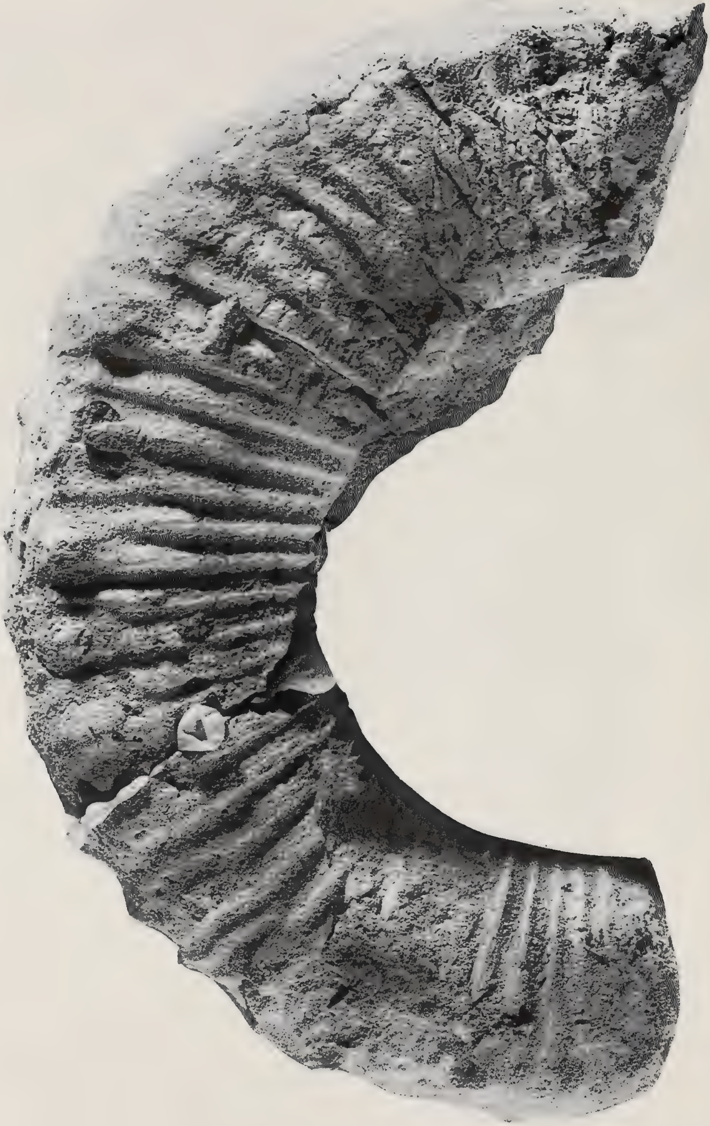

Figure 46

Didymoceras (Didymoceras?) africanum sp. nov. The holotype, SAM–PCZ7637, from locality 109c, KwaZulu, St Lucia Formation, Campanian III. × 1.

Subgenus ***Didymoceras (Eodidymoceras)*** subgen. nov.

Type species

Nostoceras hyatti Stephenson var. *mitraikyensis* Collignon (1970: 67, pl. 614 (fig. 2293)) from the middle Campanian of Madagascar and lower Campanian of KwaZulu.

Etymology

Eos, indicating the dawn or origin of the genus *Didymoceras*.

Diagnosis

Major part of shell coiled in a loose helix or possibly even criocone, body chamber curves upwards. Ornament consists of bituberculate and non-tuberculate ribs. Some ribs are both flared and bituberculate. Constrictions may be present. Early whorls possibly irregular.

Discussion

This subgenus is erected for the earliest representatives of *Didymoceras* s.l. They differ from *Didymoceras* s.s. mainly in being smaller and in having more regular, corkscrew-like coiling on the major part of the phragmocone, and the upwards-facing aperture as in the majority of *Eubostrychoceras (E.)* species. The regular ornamentation consisting of tubercles on all, or on alternate ribs, some with constrictions and flared bituberculate ribs also separates *D. (Eodidymoceras)* from *Didymoceras* s.s. This lineage appears to continue in the middle Campanian of the U.S. Western Interior as *Didymoceras cochleatum* (Meek & Hayden, 1859) and in the upper Campanian as *Didymoceras binodosum* Kennedy & Cobban, 1993). The genus *Cirroceras* Conrad, 1868 (type species *Ammonoceratites conradi* Morton, 1841: 109; 1842: 212, pl. 10 (fig. 1)) is generally regarded as a synonym of *Didymoceras*. The genus was revived, however, by Kennedy *et al.* (2000: 11) for forms coiled in a loose helix and with an upward curving aperture. Thus as far as coiling is concerned, *Cirroceras* is very close if not indistinguishable from *D. (Eodidymoceras)*. The main differences are that in *Cirroceras*, of the two rows of tubercles, those of the lower row are larger, and constrictions are absent. In addition, *Cirroceras* is only known with certainty from the upper part of the upper Campanian. If *Cirroceras* is to be considered a valid taxon, it should possibly be regarded as a subgenus of *Didymoceras*. It is possibly derived from the *D. (Eodidymoceras)* lineage.

Unfortunately our material is limited, but all three KwaZulu and Madagascan species to be described below show distinct *Allocrioceras*-like features, thus suggesting that the origins of the Nostoceratidae may be sought in that genus.

Occurrence

Lower Campanian of KwaZulu; middle Campanian of Madagascar; ?middle and upper Campanian of the U.S. Western Interior.

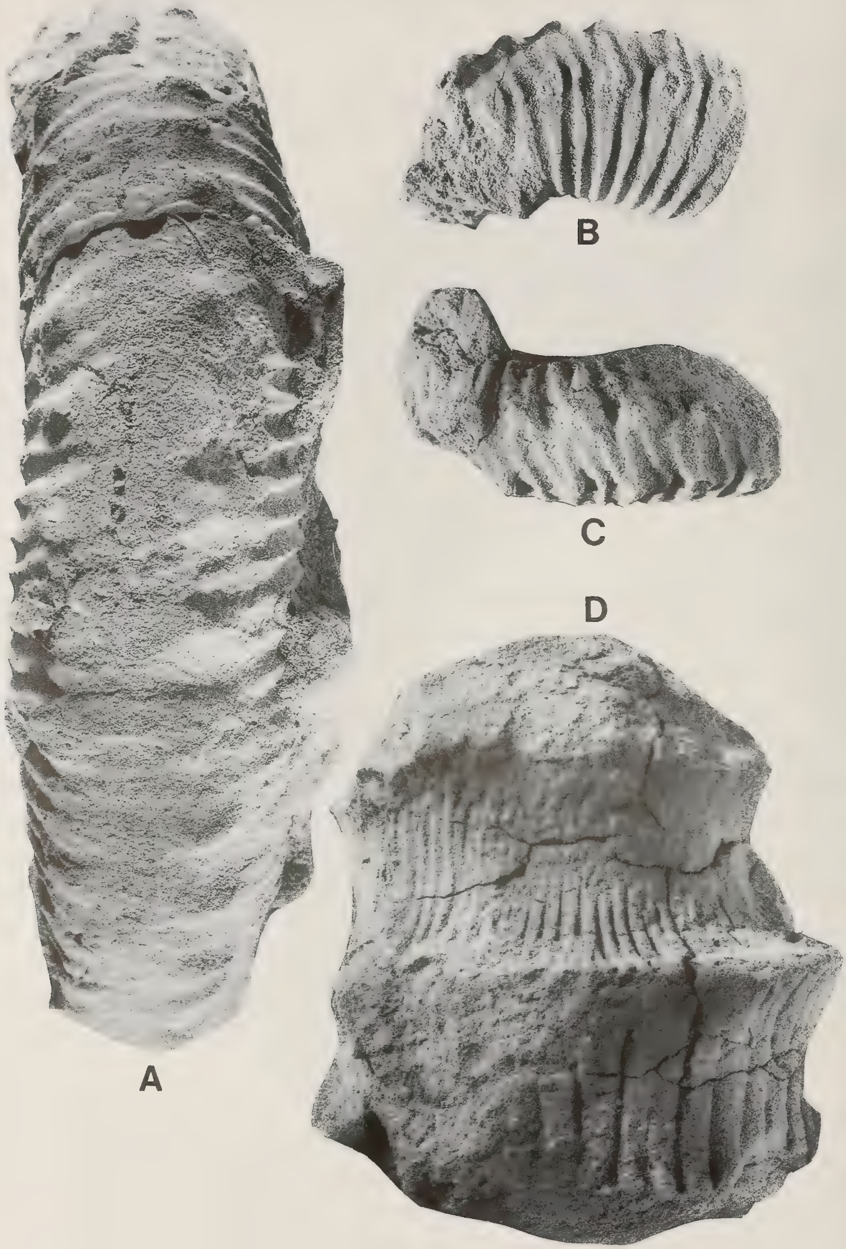

Figure 47

A–C. *Didymoceras (Didymoceras?) africanum* sp. nov. The holotype, SAM–PCZ7637 from locality 109c, KwaZulu, St Lucia Formation, Campanian III. A. The outer whorl. B–C. Fragment of inner whorls impressed into the outer whorl. Note the asymmetry of the ornamentation, indicative of low, helical rather than planispiral coiling. D. *Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). SAM–PCZ17352, probably from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b. Impression of phragmocone of specimen with acute apical angle. All × 1.

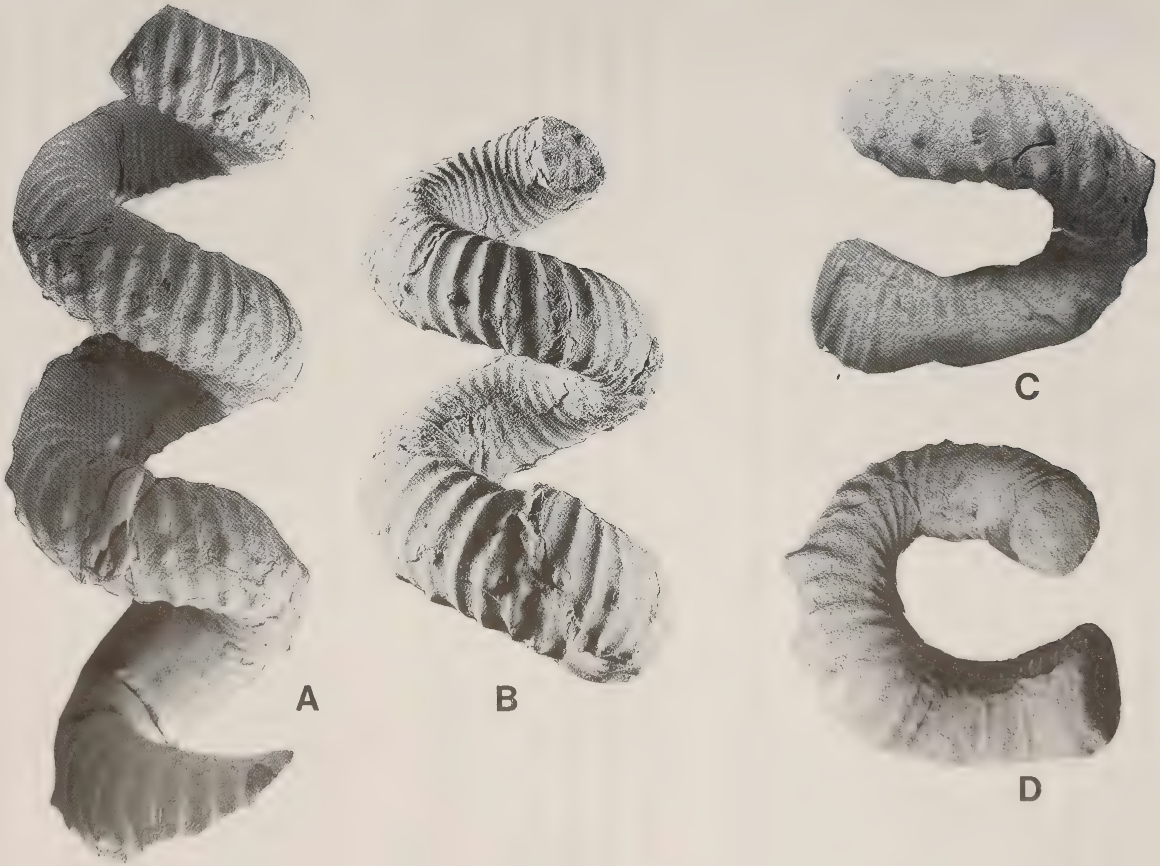

Figure 48

Didymoceras (Eodidymoceras) mitraikyense (Collignon, 1970). A–B. SAM–PCZ18754 (ex WJK 4/D) from locality 14, KwaZulu, St Lucia Formation, lower Campanian. C–D. The holotype, GD11293 from Gisement 148, Mitraiky (Antsalova), Madagascar, middle Campanian, Zone of *Pachydiscus grossouvrei*. Note upward curvature of body chamber. × 1.

Didymoceras (Eodidymoceras) mitraikyense (Collignon, 1970)

Fig. 48

?1969 *Nostoceras* sp. Collignon, p. 46, pl. 530 (fig. 2092).

1970 *Nostoceras hyatti* Stephenson var. *mitraikyensis* Collignon, p. 67, pl. 614 (fig. 2293).

1976 *Didymoceras (Didymoceras) schloenbachi schloenbachi* (Favre, 1869); Klinger, p. 67, pl. 29 (fig. 4), pl. 30 (fig. 4).

Type

Holotype is the specimen figured by Collignon (1970, pl. 614 (fig. 2092)) GD11293 (Fig. 48C–D) from the middle Campanian, of Gisement 148, Mitraiky (Antsalova), Madagascar.

Material

SAM–PCZ18754 from locality 14, KwaZulu, St Lucia Formation, lower Campanian.

Description

No new material has been found since Klinger's (1976) original description, but several pieces have been fitted together to form a helix consisting of about three and a half whorls. Coiling is sinistral, forming a regular, loose corkscrew, with the whorls separated by intervals of approximately one whorl height. The holotype (Fig. 48C–D) shows that the last part of the body chamber curves upwards in *Eubostrychoceras (E.)*-fashion.

Ornament consists of about 30 single, radial to slightly rursiradiate ribs per whorl. Each alternate rib bears two rows of tubercles, one just below midflank, and the other at the abapical edge.

Discussion

Following Wiedmann's (1962: 204) interpretation of *Helicoceras schloenbachi* Favre (1869: 30, pl. 7 (fig. 5)), Klinger (1976: 67) referred the KwaZulu material to that species. However, Blaszkiewicz (1980) and Kennedy & Summesberger (1987: 31) suggested that all Campanian specimens referred to *schloenbachi* belong elsewhere. In the case of loosely coiled specimens such as the KwaZulu material, Kennedy & Summesberger (1987: 31) suggested that they may even belong to different genera.

As far as the loose, helical coiling, and ornament on the phragmocone are concerned, *D. (Eodidymoceras) mitraikyense* is very similar to *D.* (*D.*) *puebloense* Cobban *et al.* (1997: 225, figs 2–5) from the upper Campanian of Colorado and Wyoming. That species, however, has the typical U-shaped body chamber suspended below the phragmocone, and large size of *Didymoceras* s.s.

Fragments of *D. (E.) mitraikyense* are virtually indistinguishable from helically coiled species of *Allocrioceras*, e.g. *A. billinghursti* Klinger, 1976 (see Fig. 52E–F). Again, we are not quite sure of the exact relationships between the two genera but, as suggested above, it seems to confirm our view that at least some of the Nostoceratidae can trace their origins to *Allocrioceras* during the Turonian.

A few species of *Didymoceras* show loose coiling similar to that of *D. (E.) mitraikyense*, but in all the cases the ornament is sufficiently different to distinguish between these. *D. (D.) donezianum* (Mikhailov, 1951), recently reviewed by Kennedy & Cobban (1993*c*: 137) has loose coiling in the early stages, but the body chamber becomes closely coiled. *Didymoceras (D.) navarroense* (Shumard, 1861) (see Stephenson 1941: 417, pl. 83 (figs 9–13)), and Kennedy & Cobban (1993*a*: 421, figs 12.1, 13.1–13.8, 14.1–14.4, 14.13, 14.14) has more robust ornament, and numerous fine looped and intercalatory ribs. *Didymoceras* (*D.*) *subtuberculatum* Howarth (1965: 374, pl. 7 (figs 2–6), pl. 11 (fig. 4)) has similar loose coiling on the phragmocone, and regularly-spaced, flared ribs; it may possibly be referred to *D. (Eodidymoceras).*

Occurrence

Lower Campanian of KwaZulu, lower? and middle Campanian of Madagascar.

Didymoceras (E.) howarthi sp. nov.

Figs 49, 50A, 51

Type

Holotype, by monotypy is SAM–PCZ7349 from locality 74, Die Rooiwalle, KwaZulu, St Lucia Formation, probably from the lower Campanian, but possibly uppermost Santonian.

Etymology

Named for Dr M. K. Howarth of the Natural History Museum, London.

Description

The holotype consists of two and a half whorls of a loosely coiled helix. Ornament consists of 34 minor and major ribs per whorl. These are narrow and high-crested, separated by much wider interspaces. The minor ribs bear two rows of minute tubercles, the first slightly above the midline and the other near the abapical quarter of the flanks. About 5 major flared ribs occur per whorl. These are flanked adaperturally by a wide constriction. Where sufficiently well preserved, these can also be seen to bear two rows of tiny pointed tubercles.

Discussion

With respect to the loose coiling of the phragmocone, bituberculate normal and flared ribs and constrictions, *D. (E.) howarthi* is very similar to *D. cochleatum* (Meek & Hayden 1859) (see Kennedy *et al.* 1999) from the middle Campanian of South Dakota and Wyoming and *D. binodosum* (Kennedy & Cobban 1993b) from the upper Campanian of the U.S. Western Interior and Gulf Coast. Neither of these two species, however, has as loose coiling as *D. (E.) howarthi*. It is possible that *D. (E.) howarthi* gave rise to this middle to upper Campanian lineage.

Another comparable species is *Didymoceras subtuberculatum* Howarth (1965: 374,

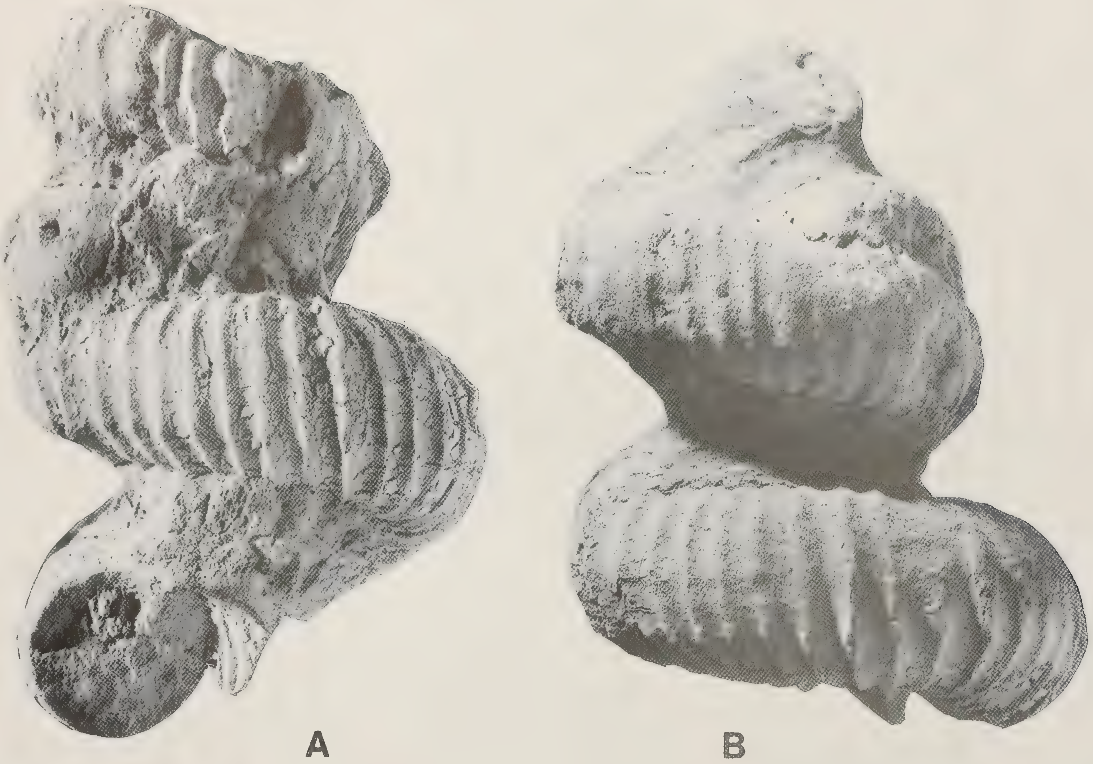

Figure 49

Didymoceras (Eodidymoceras) howarthi sp. nov. The holotype, SAM–PCZ7349 from locality 74, Die Rooiwalle, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian. Note the strong constriction with associated flared rib and weak bituberculate ornament on all ribs. × 1.

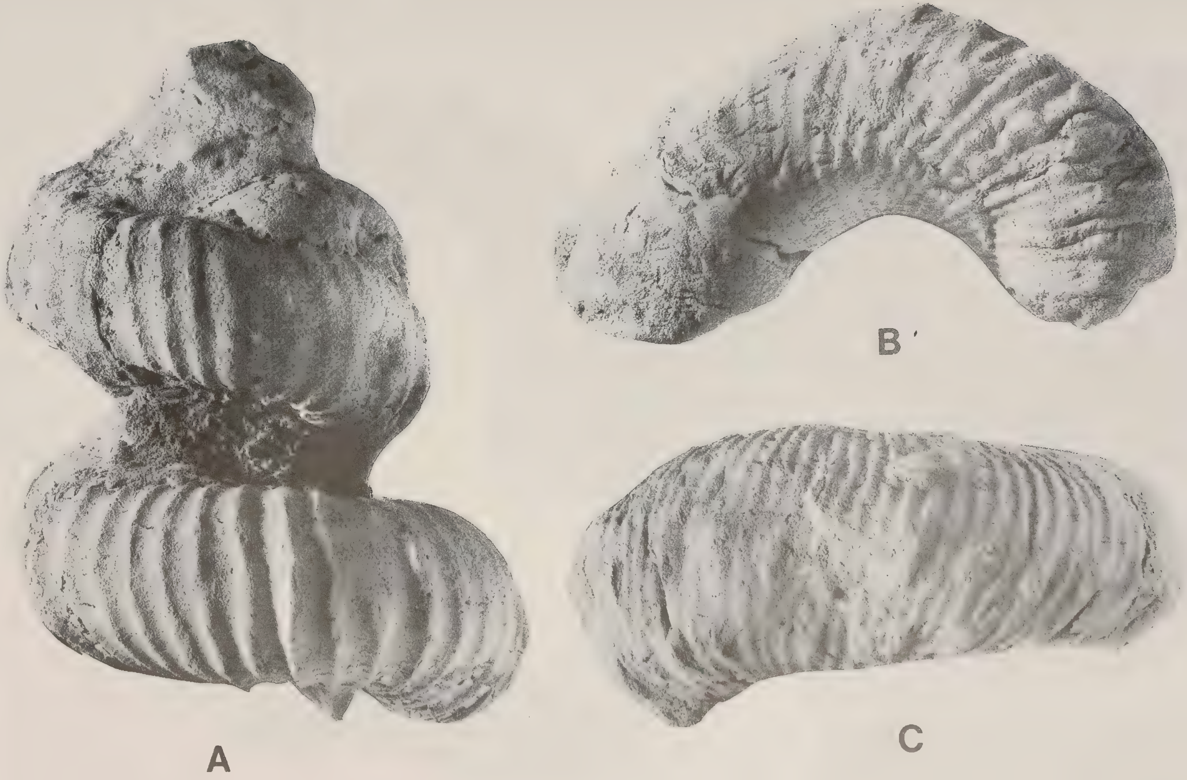

Figure 50

A. *Didymoceras (Eodidymoceras) howarthi* sp. nov. The holotype, SAM–PCZ7349 from locality 74, Die Rooiwalle, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian. B–C. *Didymoceras (Didymoceras) australis* sp. nov. NMB–D1490 from locality 109c, KwaZulu, St Lucia Formation, Campanian III. Both × 1.

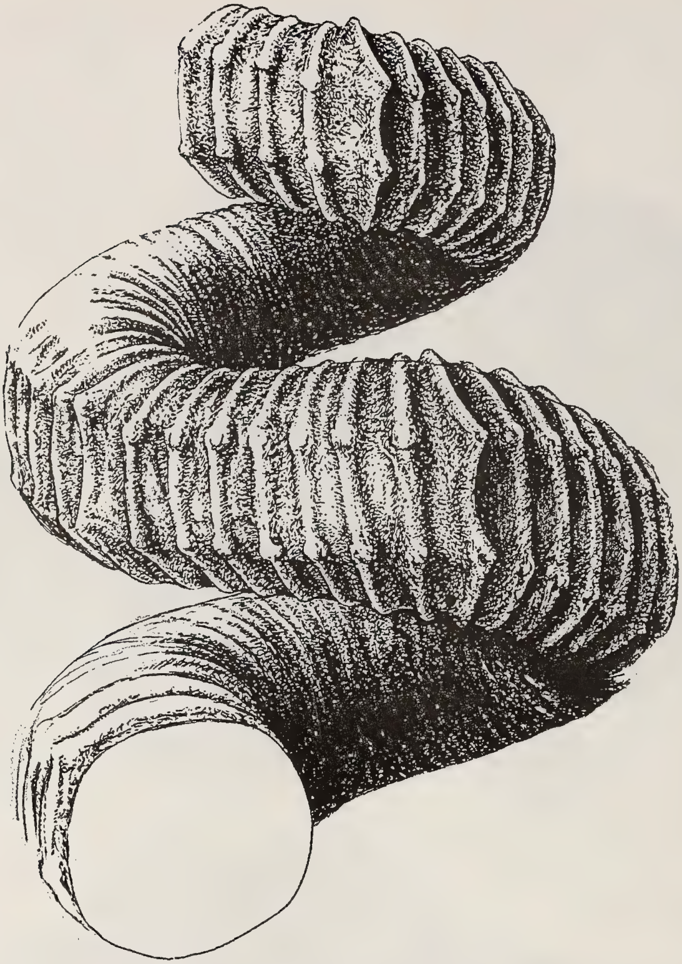

Figure 51

Didymoceras (Eodidymoceras) howarthi sp. nov. Reconstruction of the holotype, SAM–PCZ7349, by Samantha Black. × 1.

pl. 7 (figs 2–6), pl. 11 (fig. 4)) from the uppermost Campanian or basal Maastrichtian of Angola. This species could possibly also be referred to the subgenus *D. (Eodidymoceras)* as mentioned above. In *D. (D.) subtuberculatum*, however, the minor ribs are more numerous and finer, and the flared ribs far more prominent than in *D. (E.) howarthi*. Also, the two rows of tubercles in *D. (D.) subtuberculatum* are much more prominent, and placed near the base of the whorls, rather than on the flanks. The specimen from the lower Campanian of Madagascar described by Collignon (1969: 42, pl. 529 (fig. 2086)) as *Didymoceras subtuberculatum* may possibly also be referred to this species.

Occurrence

Possibly uppermost Santonian but probably lower Campanian of KwaZulu.

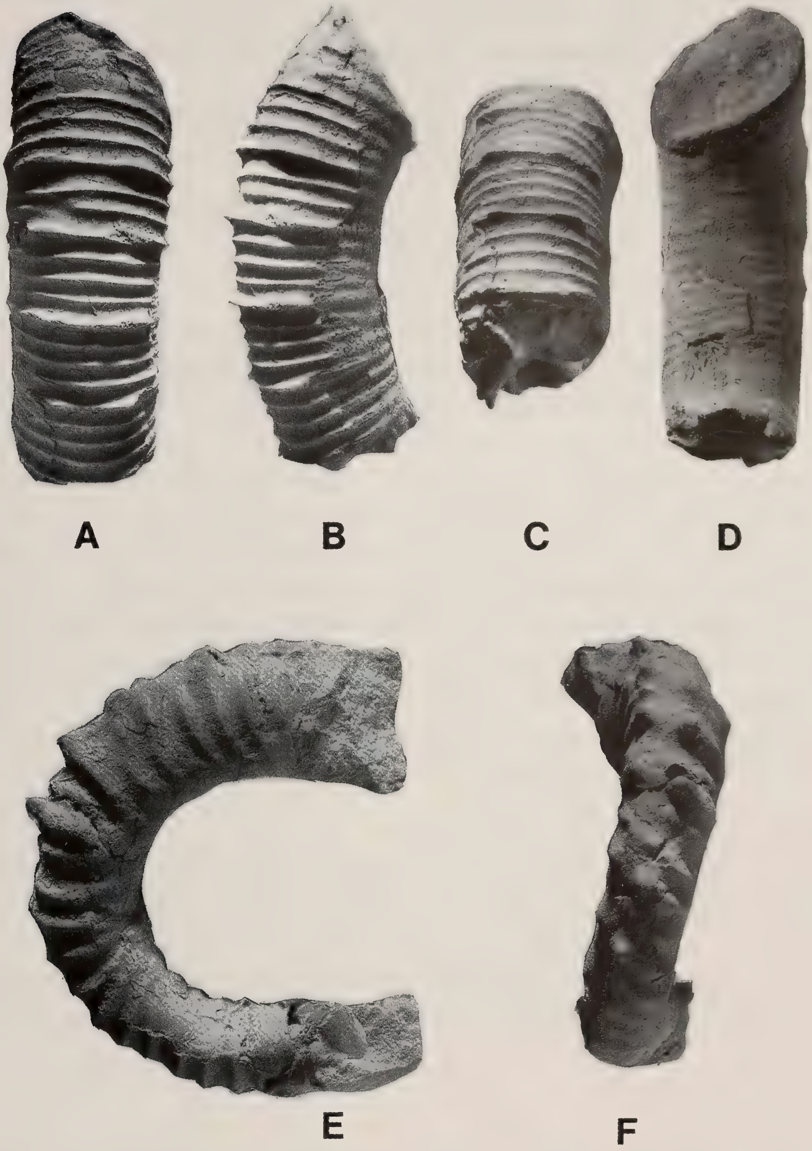

Figure 52

A–D. *Didymoceras (Eodidymoceras?)* sp. SAM–PCZ18751 (ex Z2071) from locality 105, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian. Note the bituberculate flared rib, reminiscent of *Allocrioceras* ornamentation. E–F. *Allocrioceras billinghursti* Klinger, 1976. SAM–PCZ18752 (ex Z1598) from locality 92, KwaZulu, St Lucia Formation, Coniacian II or III. Note the close resemblance to *Didymoceras (Eodidymoceras) mitraikyense* (Collignon, 1969). Both × 1.

Didymoceras (Eodidymoceras?) sp.
Fig. 8E, 52 A–D

1976	*Hyphantoceras (Madagascarites?) amapondense* (Van Hoepen); Klinger p. 71 *pars*, pl. 33 (fig. 2) only.
1994	*Allocrioceras* Cooper, p. 365, fig. 1f–g.
1997	*Eubostrychoceras (Amapondella) amapondense* (Van Hoepen); Klinger & Kennedy 1997, p. 245, fig. 15E only.
1997	'*Allocrioceras*' sp. Klinger & Kennedy, p. 246, fig. 16.

Material

SAM–PCZ18751 (ex Z2071a–b), SAM–PCZ12949 from locality 105, St Lucia Formation, KwaZulu, uppermost Santonian or basal Campanian.

Description

Unfortunately this species is based on fragments only. The most complete, SAM–PCZ18751 (Fig. 52A–D), consists of less than a third of an apparently crioceratitid whorl. The whorl section is circular; ornament consists of major, bituberculate ribs separated by three to four subsidiary, non-tuberculate ribs. The tubercles of the major ribs are extremely delicate. SAM–PCZ12949 (Fig. 8E) is a latex peel consisting of a large specimen with bituberculate major ribs and non-tuberculate intermediary ribs. Part of a *Glyptoxoceras*-like whorl occurs with this specimen. We do not know if the two specimens belong to the same individual; if they do, it suggests that the early whorls of *Didymoceras (Eodidymoceras)* may be irregular, as in later *Didymoceras* s.s. spp.

Discussion

If these specimens were found in isolation and without a Santonian/Campanian date, we would not hesitate to refer them to *Allocrioceras,* as was done by Cooper (1994, fig. 1F–G). This genus, however, is generally limited to the Cenomanian to Coniacian Stages. However, the similarities between *Allocrioceras* and *D. (Eodidymoceras)* are so striking, that we doubt if these similarities are purely homoeomorphic, as previously mentioned.

Occurrence

Upper Santonian and/or lower Campanian of Pondoland, KwaZulu and Madagascar (HCK pers. obs.)

Family Diplomoceratidae Spath, 1926
(= Family Solenoceratidae Cooper, 1994; Family Neocrioceratidae Spath, 1953)
Subfamily Diplomoceratinae Spath, 1926
(= Scalaritinae Ward, 1976)
Genus *Diplomoceras* Hyatt, 1900
[= *Eudiplomoceras* Brunnschweiler, 1966]

Type species

Baculites cylindracea Defrance, 1816 by original designation of Hyatt (1900: 160).

Diagnosis

Shell consists of three or more parallel shafts, closely spaced, but not in contact. Whorl section varies from compressed through circular to depressed. Ornament consists of fine, sharp-crested, dense ribbing. Internal moulds are generally, but not always smooth. Suture deeply incised and complex. The shell may reach very large size, with body chambers over a metre in length.

Discussion

Klinger (1976) followed Wiedmann (1962) in regarding *Glyptoxoceras* as a subgenus of *Diplomoceras*. The recent descriptions of well-preserved and abundant specimens of *Glyptoxoceras* from south India (Kennedy & Henderson 1992), Western Australia (Henderson *et al.* 1992), France (Kennedy 1992a), British Columbia (Ward & Mallory 1977) and California (Matsumoto 1959) all show that the coiling strategies in *Glyptoxoceras*, albeit very variable, differ sufficiently from those of *Diplomoceras* to warrant separate generic status.

Following the extensive revision of the type species, *D. cylindraceum* by Kennedy (1987) it appears that the genus is monospecific. All the other 'species' referred to *Diplomoceras* are either synonyms of *D. cylindraceum* or based on uninterpretable material.

The systematics, affinities, stratigraphic and geographic distribution and possible origins of the type species, *Diplomoceras cylindraceum* are discussed fully by Klinger & Kennedy (This volume 110 (4)).

Occurrence

Where precisely dated, *D. cylindraceum* typically occurs in the Maastrichtian, but there are reports of the species from the upper Campanian of Tercis, France (Küchler & Odin 2001) and Piotrawin, Poland (Machalski 1996). Other specimens, described mainly as *D. lambi* or *D. notabile* are also recorded from the Campanian, even ranging down as far as the lower Campanian (e.g. Alabushev & Wiedmann 1997).

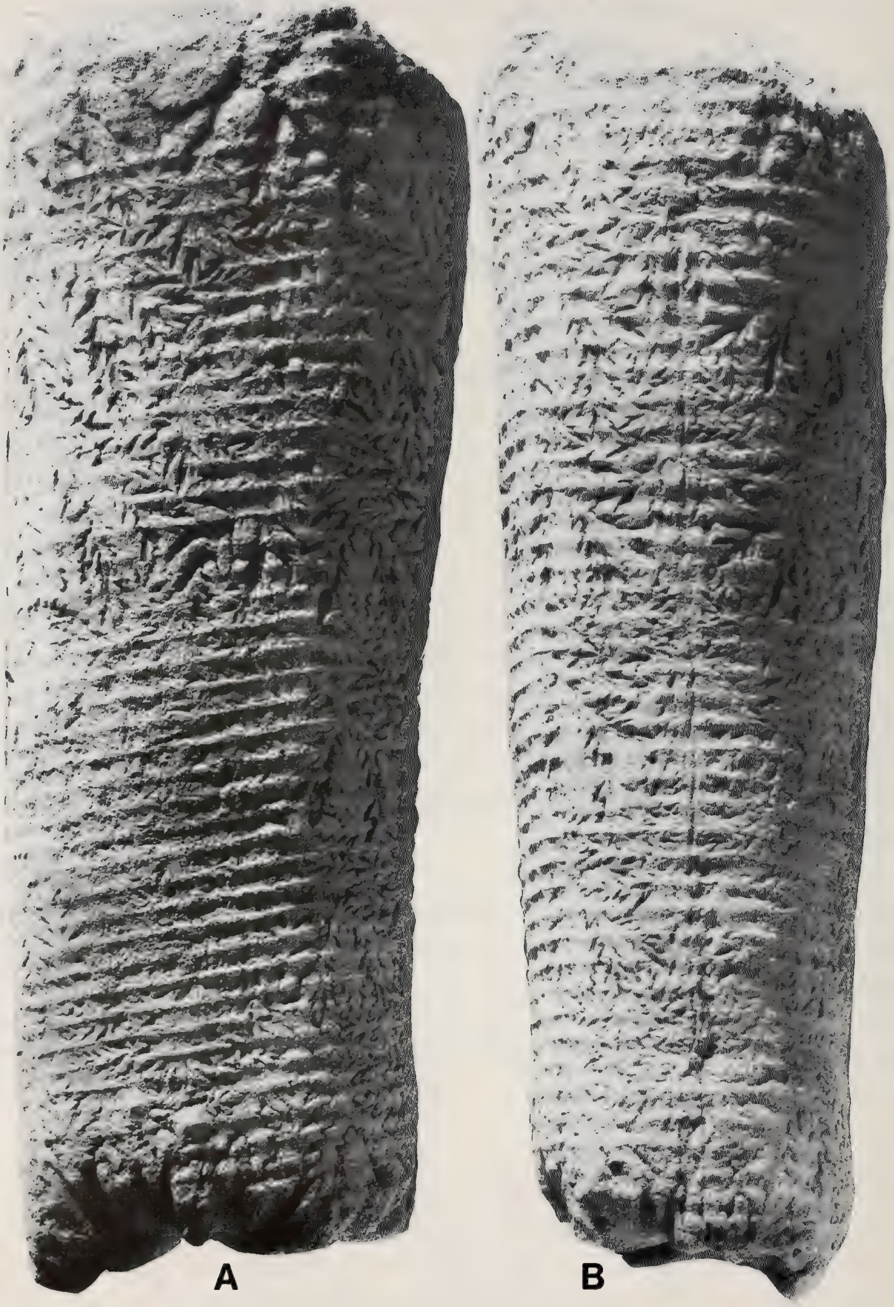

Figure 53

Diplomoceras cylindraceum (Defrance, 1816). SAM–PCZ17355 (ex SAS–A432) from locality 111, KwaZulu, St Lucia Formation, Campanian III. × 1.

Diplomoceras cylindraceum (Defrance, 1816)

Figs 53–55

1816	*Baculites cylindracea* Defrance, p. 160.
1976	*Diplomoceras (Diplomoceras) notabile* Whiteaves; Klinger, p. 82, pl. 33 (figs 2a–b, 4a–b).
1987	*Diplomoceras cylindraceum* (Defrance); Kennedy, p. 181, pl. 17 (fig. 3), pl. 18 (fig. 5), pl. 21 (figs 2–3, 5–6), pl. 22 (fig. 6), pl. 23 (figs 1–2), pl. 24 (figs 1–3), pl. 25 (figs 1–8), pl. 26 (fig. 18), pl. 33 (fig. 16), pl. 36 (fig. 6), text-figs 9–10 (with full synonymy).
1992	*Diplomoceras cylindraceum* (Defrance); Henderson *et al.*, p. 140, figs 5, 6A–E, H–K, 7.
1992	*Diplomoceras cylindraceum* (Defrance); Kennedy & Henderson, p. 704, pl. 6 (figs 1–3), text-figs 1B, 3.
1993	*Diplomoceras cylindraceum* (Defrance); Hancock & Kennedy, p. 164, pl. 15 (fig. 15), pl. 17 (figs 1–4).
1993	*Diplomoceras cylindraceum* (Defrance); Ward & Kennedy, p. 49, figs 42, 43.16, 43.17.
1997	*Diplomoceras notabile* Whiteaves; Alabushev & Wiedmann, p. 14 pl. 4 (fig. 1).
1999	*Diplomoceras cylindraceum* (Defrance); Kennedy, p. 653, figs 12.1–12.5.
2003	*Diplomoceras cylindraceum* (Defrance); Klinger & Kennedy, figs 1–9.

Type

Neotype designated by Kennedy (1987: 183, pl. 24 (figs 1–3)) is no. 10511 in the collections of the Institut Royal des Sciences Naturelles de Belgique from the upper Maastrichtian Nekum or Meersen Chalk of St Pietersberg near Maastricht in The Netherlands.

Material

SAM–PCZ7843, PCZ7943 from bed 7 at locality 20, Maastrichtian II; SAM–PCZ17355 (ex SAS–A432) from locality 111, Campanian III; SAM–PCZ9551 from locality 113, Maastrichtian a or b; SAS–A2080, SAM–PCZ12950 (ex H108/9), PCZ12951 from locality 116, Maastrichtian a, SAM–PCZ7940 from locality 20, Maastrichtian a or b; SAM–PCZ7998 from locality 124, Maastrichtian a or b; SAM–PCZ17356 (ex H105/9) from locality 116, Maastrichtian a or b; SAM–PCZ18707, SAM–PCZ7904, unlocalized from 'The Coves', Maastrichtian a or b. All from KwaZulu and all from the St Lucia Formation.

Dimensions

Specimen	MxWb	MxWh	Wb:Wh	MnWb	MnWh	Wb:Wh	Ri
PCZ12950	28	31	0.9				
PCZ7843	40	36	1.1				
PCZ9551	58	64	0.9	39	44	0.9	19
PCZ12951	57	64	0.9	45	56	0.8	16

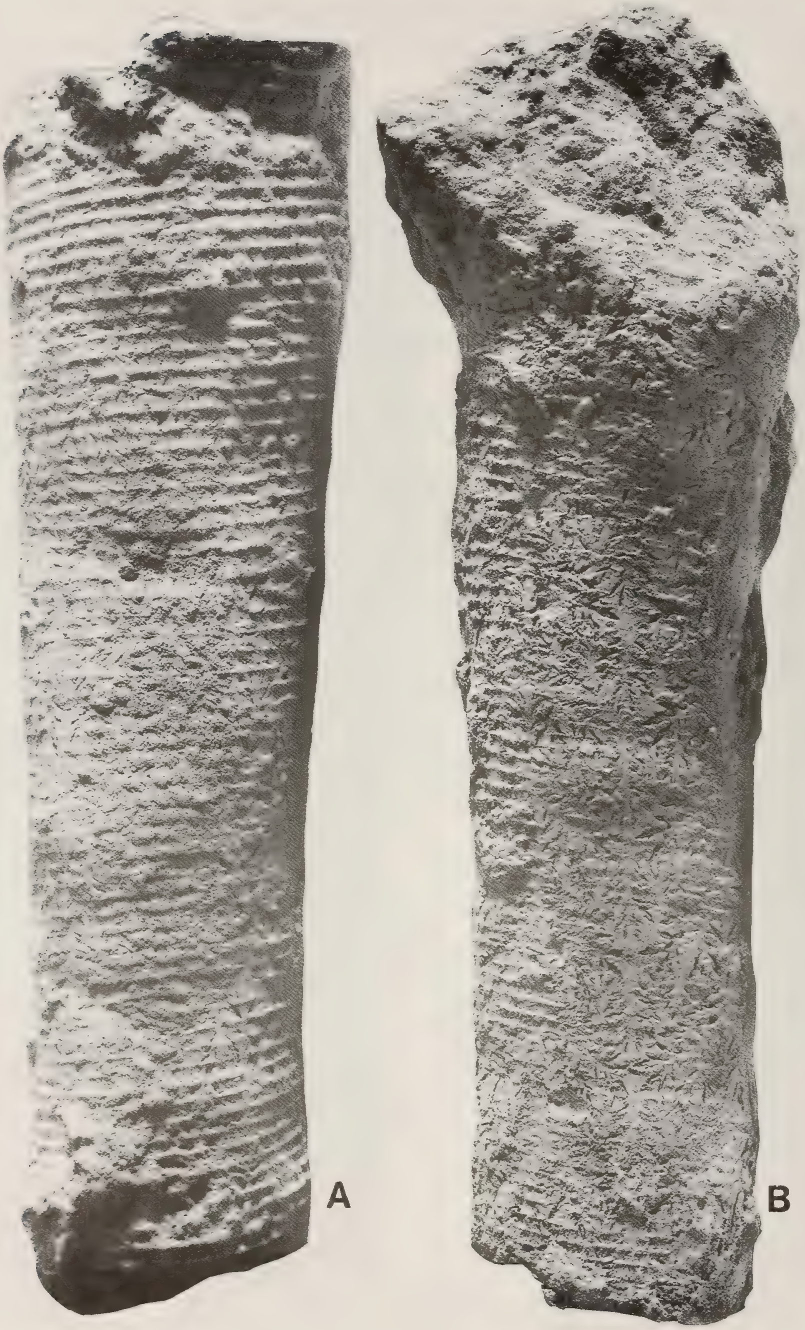

Figure 54

Diplomoceras cylindraceum (Defrance, 1816). SAM–PCZ9551 from locality 113, KwaZulu, St Lucia Formation, Maastrichtian a or b. × 1.

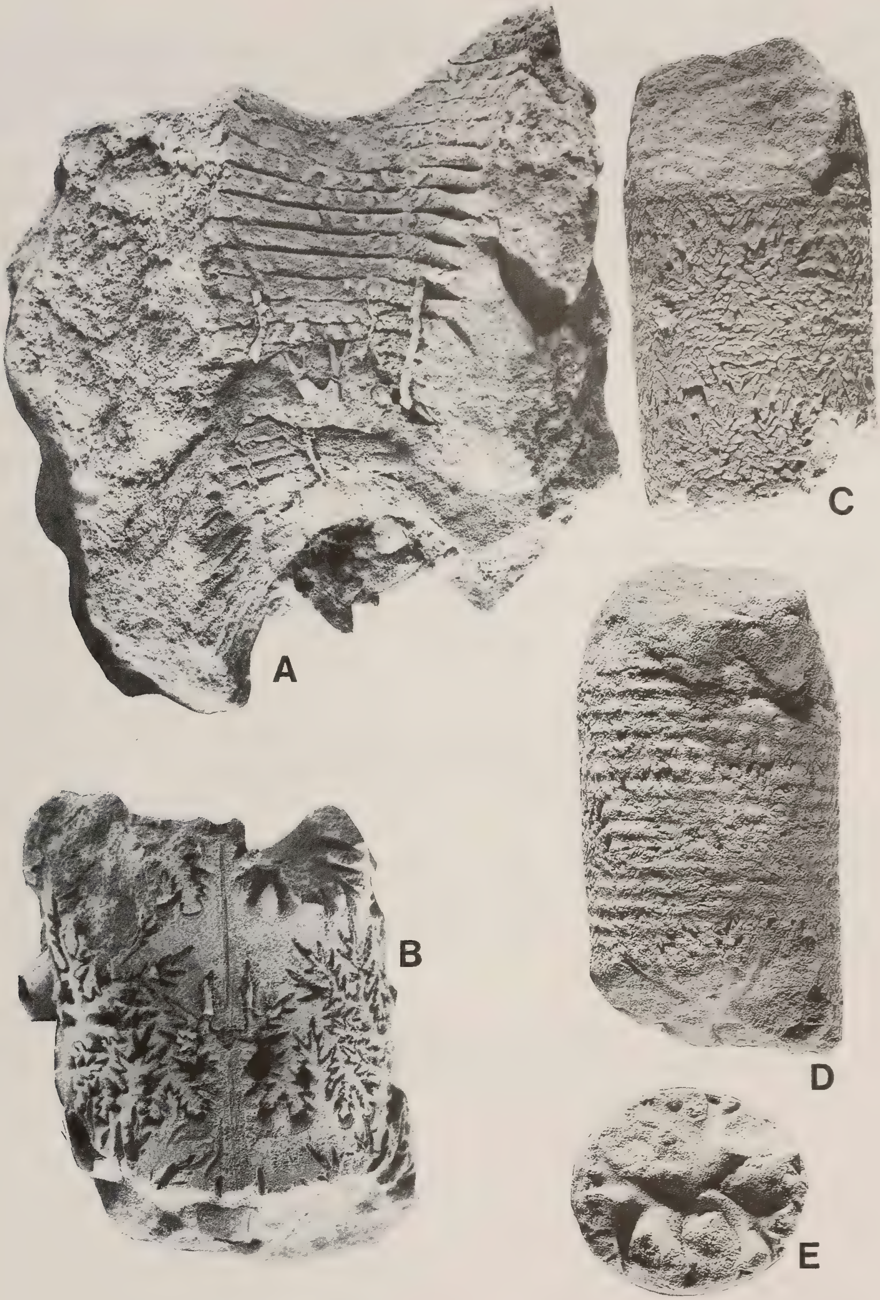

Figure 55

Diplomoceras cylindraceum (Defrance, 1816). A. SAM–PCZ7940 from locality 20, KwaZulu, St Lucia Formation, Maastrichtian a or b. B. SAM–PCZ7904, an internal mould of the phragmocone showing the typical absence of ornament. C–E. SAM–PCZ17356 (ex H105/9) from locality 116, KwaZulu, St Lucia Formation, Maastrichtian a. All × 1.

Description

All except one of our specimens are parts of the straight shafts of the phragmocone, preserved as internal moulds. The whorl section varies from depressed to near-circular to compressed. All but one of our figured specimens is ornamented by fine, *c.*16–19 ribs per whorl height. Their orientation varies from radial to distinctly rursiradiate on the larger specimens. This is rather unusual, as internal moulds of the phragmocone of this species are usually smooth, due to thickening of the nacreous layer beneath the ribs. The sutures are complex and dendritic.

Discussion

Variation in this species was described in detail by Kennedy (1987) on the basis of more than 70 specimens from the type locality and our material adds nothing new. As mentioned above, various aspects of the species are discussed extensively by Klinger & Kennedy (This volume 110 (4)).

Occurrence

Where well dated, *D. cylindraceum* is a typical Maastrichtian species, but it has been recorded from as early as Early Campanian. The species has a virtually cosmopolitan distribution; details are provided by Klinger & Kennedy (This volume 110 (4)).

Genus *Glyptoxoceras* Spath, 1925

(= *Neohamites* Brunnschweiler, 1966)

Type species

Hamites rugatus Forbes (1846: 116, pl. 11 (fig. 6)), by original designation of Spath (1925: 30).

Diagnosis

Early whorls variable, straight, criocone, open helix or turriliticone, followed by loose, planispiral elliptical or polygonal whorls. Ornament consists of simple ribs only. Aperture collared and preceded by a constriction.

Discussion

Due to the open coiling and inherent fragile nature of the shell, complete specimens of *Glyptoxoceras* are a rarity. There is great variation in density of ribbing; this, combined with the incomplete nature of the material means that the systematics of the genus are rather chaotic. At present, only the upper Maastrichtian material from south India, revised by Kennedy & Henderson (1992), and of Western Australia revised by Henderson *et al.* (1992) and *Glyptoxoceras aquisgranense* (Schlüter) from the lower Campanian, based on exquisitely preserved material from Nalzen, France (Kennedy 1992*a*) are sufficiently defined. Older, Coniacian and Santonian material from Madagascar, KwaZulu and Austria, as well as lower Campanian material from Madagascar, are difficult to separate satisfactorily.

Occurrence

Coniacian to Maastrichtian, with records from Western Europe, Poland, Russia, Madagascar, KwaZulu, India, Western Australia, British Columbia, California, New Zealand, Brazil, Chile, Jamaica and Japan.

Glyptoxoceras rugatum (Forbes, 1846)
Fig. 56C

1846 *Hamites rugatus* Forbes, p. 117, pl. 11 (fig. 2).

1992 *Glyptoxoceras rugatum* (Forbes); Kennedy & Henderson, p. 695, pl. 1 (figs 1–2, 5–16), pl. 2 (figs 10–11, 14–29), pl. 3 (figs 1–3), pl. 4 (figs 2, 12–15), text-fig. 1A, E. (*cum synon.*).

1992 *Glyptoxoceras rugatum* (Forbes); Henderson *et al.*, p. 145, (figs 8–13) (*cum synon.*).

Material

SAM–PCZ17358 from the locality exposing the contact between the base of the Uloa Formation and the top of the St Lucia Formation at Monzi (see e.g. Cooper & McCarthy 1998: 5, fig. 7a for details). Maastrichtian I or II.

Description and discussion

A single, straight fragment with a circular section and about five ribs per whorl height is the only specimen referable to this species.

This species is best known from the upper Maastrichtian of Western Australia (Henderson *et al.* 1992) and south India (Kennedy & Henderson 1992). These authors provide an extensive synonymy of the species and show that the various specific names applied, e.g. *subcompressus, nereis, circulare, nipponicum, bullarensis, giraliensis, cardabiensis, largesulcatus* and *soufoulisi* all fall within the variation of *G. rugatum.*

Occurrence

Maastrichtian of south India, KwaZulu, Brazil, possibly Chile, Western Australia, northern Spain, south-east France, The Netherlands and Belgium.

Glyptoxoceras octocostatum (Collignon, 1969)
Fig. 56A–B, D–F

1906 *Heteroceras* sp. Woods, p. 339, pl. 42 (fig. 5).

1921a *Diplomoceras*? *indicum* Spath, p. 256, pl. 23 (fig. 5).

1969 *Diplomoceras indicum* Forbes *octocostatum* Collignon, p. 45, pl. 530 (fig. 2090).

1976 *Diplomoceras (Glyptoxoceras) indicum* (Forbes); Klinger, p. 79, pl. 34 (figs 3–5).

Material

SAM–PCZ18739 and SAM–PCZ18741 from an unspecified horizon at Mkweyane (Umkwelane Hill), St Lucia Formation, Santonian or Campanian; SAM–PCZ17357 and

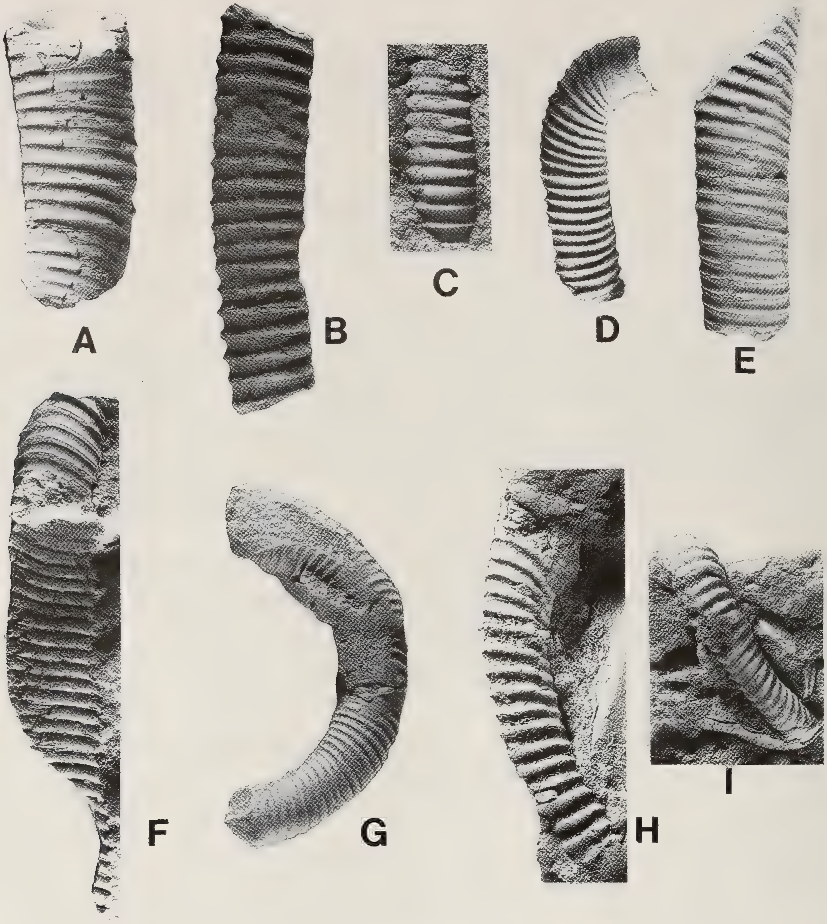

Figure 56

A–B, D–F. *Glyptoxoceras octocostatum* (Collignon, 1969). A. SAM–PCZ18739. D. SAM–PCZ18741. Both from Mkweyane (Umkwelane Hill), KwaZulu, St Lucia Formation, upper Santonian or lower Campanian. B. SAM–PCZ18740 from locality 105, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian. E–F. SAM–PCZ17357 from locality 105, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian. C. *Glyptoxoceras rugatum* (Forbes, 1846). SAM–PCZ17358 from below the base of the Uloa Formation at Monzi, KwaZulu, St Lucia Formation, Maastrichtian. G. *Neoglyptoxoceras collignoni* nom. nov. SAM–PCZ18742 from locality 109, KwaZulu, St Lucia Formation, Campanian II or III. H–I. *Scalarites* sp. H. SAM–PCZ18738. I. SAM–PCZ7961, both from locality 72, KwaZulu, St Lucia Formation, Coniacian II. All × 1.

SAM–PCZ18740 (ex Z2071) from locality 105, St Lucia Formation, uppermost Santonian or basal Campanian; SAM–PCZ9923 from locality 18, KwaZulu, St Lucia Formation, Santonian.

Description and discussion

The material consists of curved fragments of a species which may be referred to *G. octocostatum.* The whorl section is rounded and, as the name implies, ornament consists of

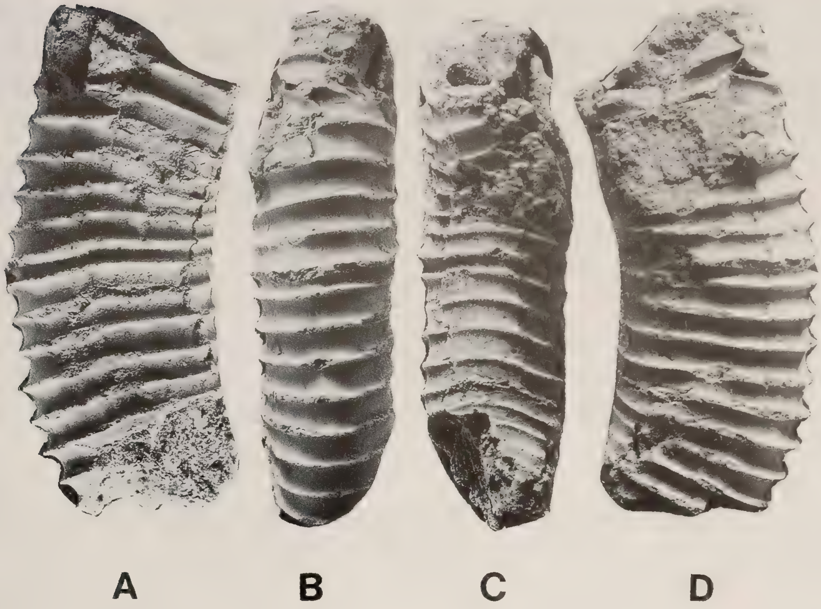

Figure 57

Glyptoxoceras texanum Kennedy, Landman & Cobban, 2001. SAM–PCZ12955 (ex H179/20) from locality 6, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian. × 1.

about eight sharp ribs per whorl height. As indicated by Kennedy & Henderson (1992) and Henderson *et al.* (1992), *G. indicum* is a typical Maastrichtian species, and not conspecific with the Santonian and/or Campanian material referred to this species by e.g. Klinger (1976: 79).

Occurrence

Uppermost Santonian and/or basal Campanian of Pondoland and KwaZulu, and lower Campanian Madagascar.

Glyptoxoceras texanum Kennedy, Landman & Cobban, 2001
Fig. 57

1976	*Diplomoceras (Glyptoxoceras) subcompressum* (Forbes); Klinger, p. 80, pl. 34 (fig. 6).
2001	*Glyptoxoceras texanum* Kennedy, Landman & Cobban, p. 7, (fig. 4).

Material

SAM–PCZ12955 (ex H179/20) from spoil heaps at excavations for a bridge at locality 6, St Lucia Formation, upper Santonian or basal Campanian.

Description and discussion

The specimen differs from all others referred to *Glyptoxoceras* in southern Africa in having a distinctly compressed whorl section (Wb:Wh = 0.7), about six ribs per whorl height and a distinct constriction. Even though we only have a single specimen, the dimensions, ornamentation and stratigraphic occurrence are identical to the species recently described by Kennedy *et al.* (2001: 7) from the top of the Blossom Sand in Texas as *Glyptoxoceras texanum*.

Klinger (1976: 80) previously referred the specimen to *G. subcompressum*, but that species has thus far only been accurately recorded from the upper Maastrichtian and therefore can not be the same as the KwaZulu specimen.

Occurrence

Uppermost Santonian or basal Campanian of KwaZulu, upper Santonian of Texas.

Genus *Scalarites* Wright & Matsumoto, 1954

Type species

Helicoceras scalare Yabe (1904: 9, pl. 3 (fig. 2)), by original designation of Wright & Matsumoto (1954: 115).

Diagnosis

Early straight shaft with constrictions followed by loose elliptical coils ornamented by simple ribs with occasional flared, non-tuberculate ribs and occasional constrictions.

Discussion

Scalarites is amongst the oldest diplomoceratids. *Scalarites densicostatus* Matsumoto (1977: 349, pl. 57 (fig. 1), pl. 61 (fig. 6)) already occurs in the middle Turonian. It differs from other *Scalarites* in having *Diplomoceras*-like coiling. Matsumoto (1977: 350) suggested that it might be ancestral to *Polyptychoceras obstrictum*.

Differences between *Glyptoxoceras* and *Scalarites* may be slight. We suspect that some of the Coniacian and Santonian '*Glyptoxoceras*' may be representatives of *Scalarites*.

Occurrence

The genus first appears in the middle Turonian and persists to the Santonian. It is best known from Hokkaido, but is also known from California, Morocco, northern Germany, Colombia and KwaZulu.

Scalarites sp.
Fig. 56H–I

Material

SAM–PCZ18738 (ex SAS–A1997) and SAM–PCZ7961, both from locality 72, St Lucia Formation, Coniacian II.

Description and discussion

Two body chamber fragments of what appear to be *Scalarites* are available. SAM–PCZ118738 is associated with an evolute peroniceratid. Both specimens are crushed, but the whorl section seems to be higher than wide. Ornament consists of rounded, prorsiradiate ribs, *c.* three per whorl height. Towards the larger end, the ribs become progressively prorsiradiate.

Occurrence

Coniacian II of KwaZulu.

Genus *Neoglyptoxoceras* Collignon, 1969
(= ?*Epiglyptoxoceras* Collignon, 1969)

Type species

Neoglyptoxoceras magnificum Collignon (1969: 30, pl. 523 (fig. 2065), p. 35, pl. 526 (figs 2074–2075)) by original designation of Collignon (1969: 35).

Diagnosis

Neoglyptoxoceras forms large, loose open criocone to aspinoceratid coils; some may form a low, loose helix. It is ornamented by ribs only and may have a very complex suture line. The whorl section varies from ovoid to circular. No constrictions have been observed.

Discussion

The main difference between *Neoglyptoxoceras* and *Glyptoxoceras* is the larger size of the former. A detailed discussion of the genus and its affinities are given by Klinger & Kennedy (This volume 110 (4)).

Occurrence

Lower and middle Campanian of Madagascar and middle Campanian of KwaZulu.

Neoglyptoxoceras collignoni nom. nov.
Fig. 56G

1970	*Neoglyptoxoceras serta* (Müller & Wollemann); Collignon, p. 15, pl. 613 (figs 2286–2288).
1970	?*Neoglyptoxoceras* sp. aff. *serta* (Müll. et Woll.); Collignon, p. 15, pl. 613 (fig. 2289).
2003	*Neoglyptoxoceras* sp. cf. *N. serta* Collignon 1969 *non* Müller & Wolleman, 1906; Klinger & Kennedy, fig 10c.

Type

The holotype is the specimen figured by Collignon (1970, pl. 613 (fig. 2286)) from the middle Campanian of Gisement 203, Coupe d'Andimaka, Belo sur Tsiribihina, Madagascar.

Etymology

Named after the late General M. Collignon.

Material

SAM–PCZ18742 from locality 109C, KwaZulu, St Lucia Formation, Campanian III?

Description and discussion

Half a criocone whorl with a rib density of about 6 per whorl height appears identical with Collignon's figured material from the middle Campanian of Madagascar.

Collignon (1970: 15) originally identified his Madagascan specimens with Müller & Wollemann's (1906: 20, pl. 9 (fig. 3), pl. 10 (figs 1–4)) *Crioceras serta*, as *Neoglyptoxoceras*. Müller & Wollemann (1906: 21), however, clearly state that in later stages of growth, larger, flared ribs start appearing at regular intervals. Because of this latter feature, *Crioceras serta* cannot be referred to *Neoglyptoxoceras*. This type of ornamentation is reminiscent of *Eubostrychoceras (Amapondella)*.

The coiling of *N. collignoni* is very similar to some *Eubostrychoceras*, but the generally much larger size may separate it from loosely coiled *Eubostrychoceras*.

Occurrence

Middle Campanian of Madagascar and Campanian III of KwaZulu.

Genus *Neocrioceras* Spath, 1921*b*
Subgenus *Neocrioceras (Neocrioceras)* Spath, 1921*b*

Type species

Neocrioceras cf. *spinigerum* Jimbo, 1894 by original designation of Spath (1921*b*: 51).

Diagnosis

Initial loose helix followed by open spiral and some with J-shaped body-chamber. Ribs, some stronger and with lateral and ventral tubercles.

Discussion

Spath erected the genus *Neocrioceras* and designated as 'genotype' (type species) part of a helically coiled fragment which he tentatively identified as *Neocrioceras* cf. *spinigerum* (here refigured as Fig. 63C–E). This specimen is from the type locality of the Mzamba Formation in Pondoland, presumably from the upper Santonian part of the section. It is, in fact, part of *N. (Schlueterella) compressum* Klinger, 1976. Diener (1925: 192) subsequently designated *Neocrioceras (N.) spinigerum* Jimbo (1894: 184, pl. 24 (figs 1–1b)) as type species of *Neocrioceras*. This has caused considerable confusion in interpreting *Neocrioceras*. Matsumoto (*in* Matsumoto *et al.* 1986) described and figured a suite of specimens of *Neocrioceras (N.) spinigerum* from the Santonian of Hokkaido. These show that *N. (N.) spinigerum* is coiled in an open, planispiral criocone throughout. This, however, is in contrast to Spath's original concept of the genus—i.e. helical early whorls and possibly an uncoiled straight shaft (as in *Ancyloceras pseudoarmatum* Schlüter 1876: 164, pl. 43 (figs 8–9)). Apart from the original material described by Spath, no additional specimens of *Neocrioceras* cf. *spinigerum* (i.e. *N. (Schlueterella) compressum*) have been found at Mzamba.

Occurrence

Neocrioceras s.s. is only definitely known from the Turonian to Santonian and possibly lower Campanian of Japan and Saghalien, and the Coniacian of KwaZulu. Records from the lower Santonian of the Gosau as *Neocrioceras maderi* by Immel *et al.* (1982: 24, pl. 9 (fig. 2), pl. 11 (figs 1–2)) are regarded as doubtful *Neocrioceras* by Matsumoto *in* Matsumoto *et al.* (1986: 468), a view not supported here.

Neocrioceras (Neocrioceras) annelisae sp. nov.

Fig. 58

Type

Holotype by monotypy is SAM–PCZ9809 from locality 72, KwaZulu, St Lucia Formation, Coniacian III.

Etymology

Named after Annelise Crean (S.A. Museum) who patiently prepared the specimen.

Description

The holotype is septate throughout. Coiling appears to be in an open criocone. The whorl section is elliptical, higher than wide with a Wb:Wh ratio of 16:21 (0.76) and 20:24 (0.83) at the smaller and larger ends respectively.

The ornamentation of the species is very distinctive. Fine ribs occur on the flanks and over the dorsum. These are slightly prorsiradiate on the flanks and radial over the dorsum and uniformly strong throughout. A row of large clavate tubercles occurs on either side of the venter, and a second row just above mid-flank. The ventral and ventrolateral tubercles are arranged in sets of three. Starting from the abapertural end, the first ventral tubercle is smallest, the second about twice as large as the first and distinctly clavate. The third is the largest of the three and about twice as large as the preceding tubercle and distinctly clavate. It has a groove running along the lateral flank, suggesting a bipartite origin. The ventrolateral tubercles show a similar increase in size, but they are much smaller than the ventral ones. The third ventrolateral tubercle also shows a slight radial groove on the flanks, similar to that of its ventral counterpart.

Ventrally, the tubercles are connected in a series of adaperturally curved looped ribs. The ventral and ventrolateral tubercles are joined by irregularly distributed ribs; some are connected by irregular loops whereas others are connected in a zigzag fashion. About three to four intermediary ribs occur between these sets of tubercles. Dorsally, two to four ribs connect with the ventrolateral tubercles.

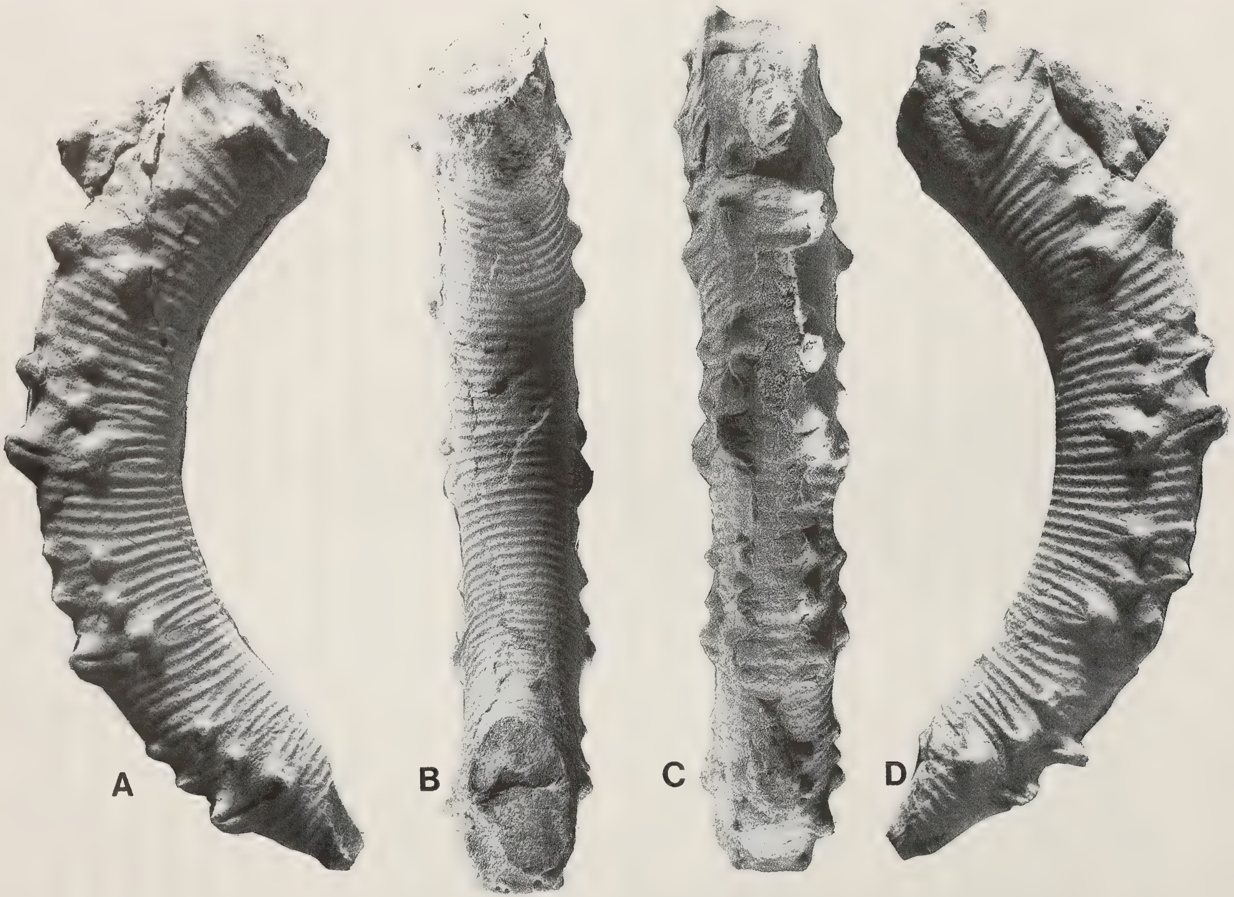

Figure 58

Neocrioceras (Neocrioceras) annelisae sp. nov. The holotype, SAM–PCZ9809 from locality 72, KwaZulu, St Lucia Formation, Coniacian III. × 1.

Discussion

Even though this species is represented by a single specimen only, the unique mode of ornamentation consisting of sets of three tubercles arranged in order of increasing size clearly distinguishes *N.* (*N.*) *annelisae* from all other representatives of *Neocrioceras.* The open, criocone coiling and lack of clearly thickened ribs suggests that the species is best referred to *Neocrioceras* s.s. rather than to *N. (Schlueterella).*

The closest match with the present species is *Kawashitaceras dentatum* Matsumoto & Obata (1981: 115, pl. 1 (fig. 1), pl. 2 (fig. 1)); also Matsumoto (1984, fig. 1) from the upper Turonian of Hokkaido. Here, however, the ventral and ventrolateral tubercles are each situated on a wide base and their crests are serrated and staggered.

Occurrence

Coniacian III of KwaZulu.

Subgenus *Neocrioceras (Schlueterella)* Wiedmann, 1962

Type species

Ancyloceras pseudoarmatum Schlüter 1872 by original designation of Wiedmann (1962: 205).

Diagnosis

Open spiral or helix followed by ancyloceratid coiling. Tuberculate ribs, with four rows of tubercles, more prominent than intercalatory, non-tuberculate ones.

Discussion

Matsumoto & Miyauchi (1984: 59) and Matsumoto *in* Matsumoto *et al.* (1986: 469) have discussed the affinities of *Neocrioceras (Schlueterella)* and *Neocrioceras (Neocrioceras)*. Some species, which had been referred to *Neocrioceras (Schlueterella),* e.g. *N. (S.) riosi* Wiedmann (1962: 205, pl. 12 (fig. 7)) from the Campanian of northern Spain and *S. multinodosum* (Schlüter 1872: 106, pl. 32 (figs 1–2)); Wright 1979: 293, pl. 2 (figs 4–5)) from the Turonian of Germany and England are best referred to *Pseudoxybeloceras,* as pointed out in part by Klinger (1976: 74).

Occurrence

The subgenus first appears in the middle Coniacian of Wyoming, but is most common in the Santonian to Campanian, with records from KwaZulu, Pondoland, Madagascar, California, northern Germany, Sweden, France, Romania and Hokkaido.

Neocrioceras (Schlueterella) compressum Klinger, 1976
Figs 59, 60A–C, 61

1921*b* *Neocrioceras* cf. *spinigerum*, Jimbo sp.; Spath, p. 52, pl. 7 (fig. 6a–c).
1976 *Neocrioceras (Schlueterella) compressus* Klinger, p. 74, pl. 33 (fig. 5), text-figs 8j, 10g.

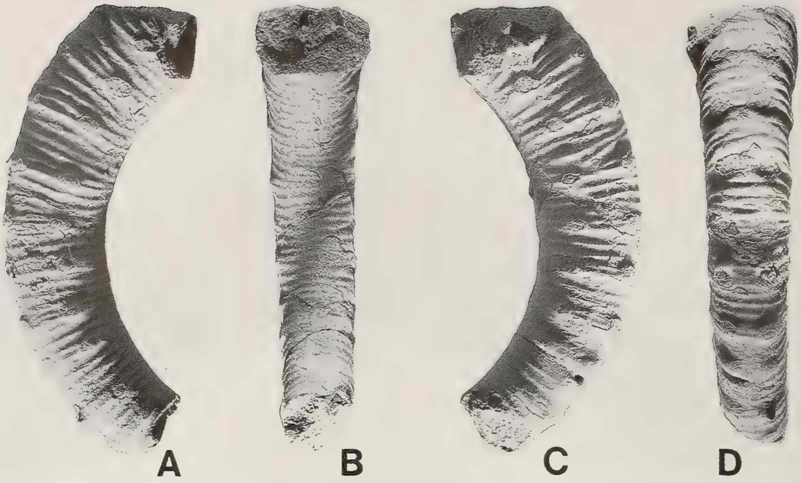

Figure 59

Neocrioceras (Schlueterella) compressum Klinger, 1976. SAM–PCZ17363 from locality 74, KwaZulu, St Lucia Formation, Santonian I. × 1.

1982	*Neocrioceras (Schlueterella) compressum* Klinger; Immel *et al.* p. 25, pl. 9 (fig. 3), pl. 10 (figs 1–4), pl. 11 (fig. 3).
1991*b*	*Neocrioceras (Schlueterella) compressum* Klinger; Kennedy & Cobban, p. 65, pl. 10 (figs 1–2), pl. 12 (figs 4–7), text-fig. 25c.
1995	*Neocrioceras (Schlueterella) compressum* Klinger; Kennedy, p. 430, pl. 27 (figs 13–15), pl. 29 (figs 4–7).

Type

Holotype is SAS–19/1, the specimen figured by Klinger (1976, pl. 33 (fig. 5), text-figs 8j, 10g) from locality 94, KwaZulu, St Lucia Formation, Santonian I.

Material

Apart from the holotype, the specimen described and figured by Spath (1921*b*, pl. 7 (figs 6a–c)) as *Neocrioceras* cf. *spinigerum* and SAM–PCZ17363 from locality 74, Santonian I and SAM–PCZ17364 from locality 79, Coniacian V, KwaZulu, St Lucia Formation.

Description and discussion

It is now clear that Spath unknowingly had *Schlueterella* in mind when he proposed the genus *Neocrioceras*. The 'genotype' (type species) of Spath's *Neocrioceras* is in fact a good example of *Neocrioceras (Schlueterella) compressum* Klinger, 1976. A crushed body chamber fragment from locality 79 (Fig. 60A–C) has ornament comparable to that described and figured by Immel *et al.* (1982) from the Santonian of Austria, especially their (1982, pl. 10 (fig. 3)) specimen with few intercalatory ribs.

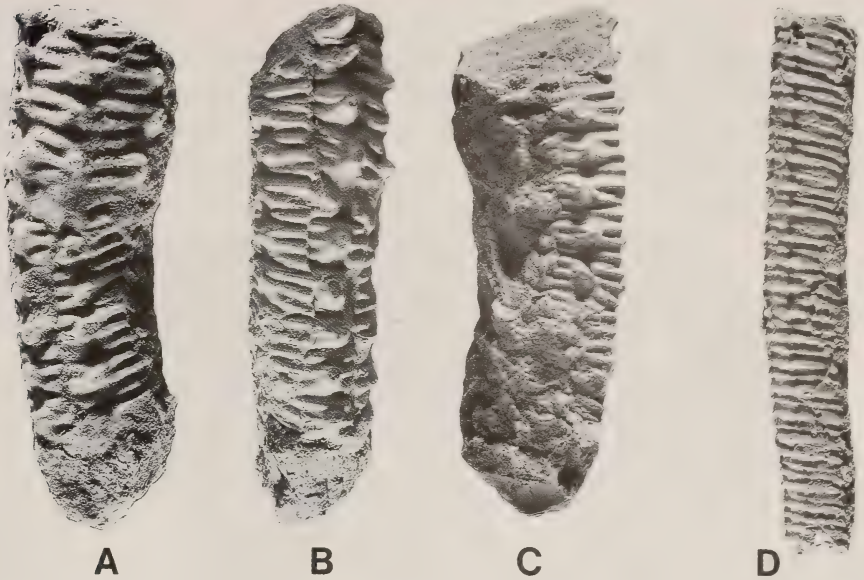

Figure 60

A–C. *Neocrioceras (Schlueterella) compressum* Klinger, 1976. SAM–PCZ17364 from locality 79, KwaZulu, St Lucia Formation, Coniacian V. D. *Pseudoxybeloceras (Pseudoxybeloceras) quadrinodosum* (Jimbo, 1894). SAM–P1411 from an unspecified horizon at the type section of the Mzamba Formation, the Mzamba River Estuary, Eastern Cape Province, locality 1, upper Santonian or lower Campanian. Both × 1.

Occurrence

Upper Coniacian and lower Santonian of KwaZulu, lower Santonian of Austria, middle Coniacian of Wyoming and Santonian of California. It is also known, but as yet undescribed from Japan (Matsumoto & Miyauchi 1984: 63) and Madagascar (H.C.K. pers. ob.) (Fig. 61).

Subfamily Polyptychoceratinae Matsumoto, 1938
(*nom. transl.* Wiedmann, 1962, *ex* Polyptychoceratidae Matsumoto, 1938)
Genus *Pseudoxybeloceras* Wright & Matsumoto, 1954

Type species

Hamites quadrinodosus Jimbo, 1894 by original designation of Wright & Matsumoto (1954: 119).

Diagnosis

Shell consists primarily of straight or curved shafts connected by U-bends. Ribbing may be bi- or quadrituberculate; in some forms major ribs develop on the body chamber.

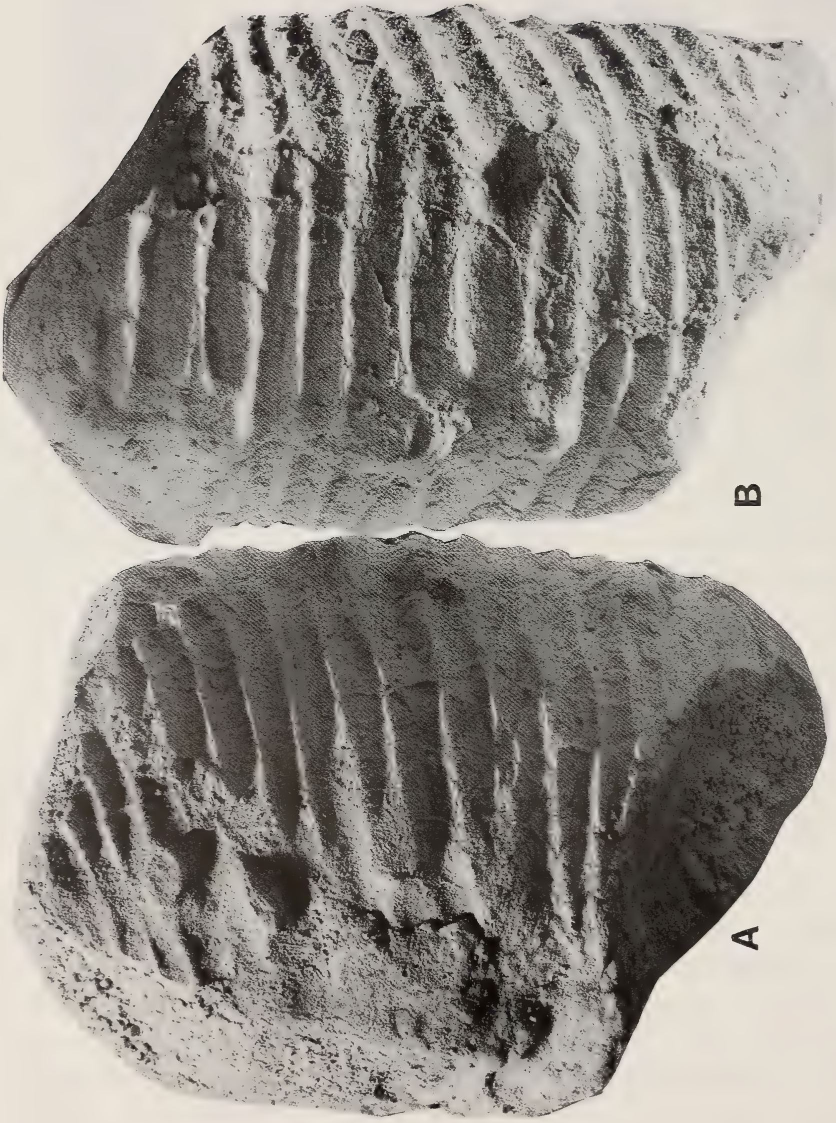

Figure 61

Neocrioceras (Schlueterella) compressum Klinger, 1976. GD, unregistered, a giant specimen from Gisement 275, middle Santonian of Madagascar. × 1.

Discussion

We follow Klinger (1976) in regarding *Parasolenoceras* Collignon, 1969 and *Christophoceras* Collignon, 1969 (of which *Cyphoceras* Ward & Mallory 1977 is a synonym) as subgenera of *Pseudoxybeloceras*. This arrangement was also followed by Matsumoto & Morozumi (1980: 19). The genus *Lewyites* Matsumoto & Miyauchi, 1984 (type species *Idiohamites* (?) *oronensis* Lewy, 1969) may possibly also be included as a subgenus in *Pseudoxybeloceras*.

Subgenus *Pseudoxybeloceras (Pseudoxybeloceras)* Wright & Matsumoto, 1954

Type species

Hamites quadrinodosus Jimbo, 1894 by original designation of Wright & Matsumoto (1954: 119).

Diagnosis

Straight or curved shafts connected by U-bends. Ribbing uniform throughout. Initial ornament may consist of ventral tubercles on ribs only, but soon changes to ventral and ventrolateral on every rib.

Occurrence

The subgenus has been recorded from the upper Turonian to possibly Maastrichtian with records from Austria, Germany, France, Romania, Pondoland, KwaZulu, Madagascar, New Zealand, U.S. Western Interior, California, British Columbia, Alaska, Hokkaido and Saghalien.

Pseudoxybeloceras (Pseudoxybeloceras) quadrinodosum (Jimbo, 1894)
Figs 60D, 62

1894	*Hamites quadrinodosus* Jimbo, p. 39, pl. 7 (figs 3–4).
1921	*Hamites amapondensis* Van Hoepen, p. 15, pl. 3 (figs 5–6), text-fig. 9.
1921*b*	*Oxybeloceras*? cf. *quadrinodosum* (Jimbo); Spath, p. 50, pl. 7 (figs 2a–b).
1954	*Pseudoxybeloceras quadrinodosum* (Jimbo); Wright & Matsumoto, p. 120, pl. 7 (fig. 6), text-figs 6, 9–12.
1974	*Pseudoxybeloceras quadrinodosum* (Jimbo); Szász, p. 193, pl. 1 (figs 1–4), pl. 2 (figs 1–3), pl. 3 (fig. 1), text-fig. 2.
1976	*Pseudoxybeloceras* sp. A. Klinger, p. 77, pl. 34 (fig. 1a–b).
1977	*Pseudoxybeloceras quadrinodosum* (Jimbo); Matsumoto, p. 345, pl. 57 (fig. 2), pl. 61 (fig. 4).
1977	*Pseudoxybeloceras quadrinodosum* (Jimbo); Ward & Mallory, p. 611, text-fig. 2.
1982	*Pseudoxybeloceras quadrinodosum* (Jimbo); Szász, p. 49, pl. 2 (figs 2a–b), pl. 3 (fig. 3a–b).
1994	*Pseudoxybeloceras amapondense* van Hoepen; Cooper, (figs 1h–i, 2).

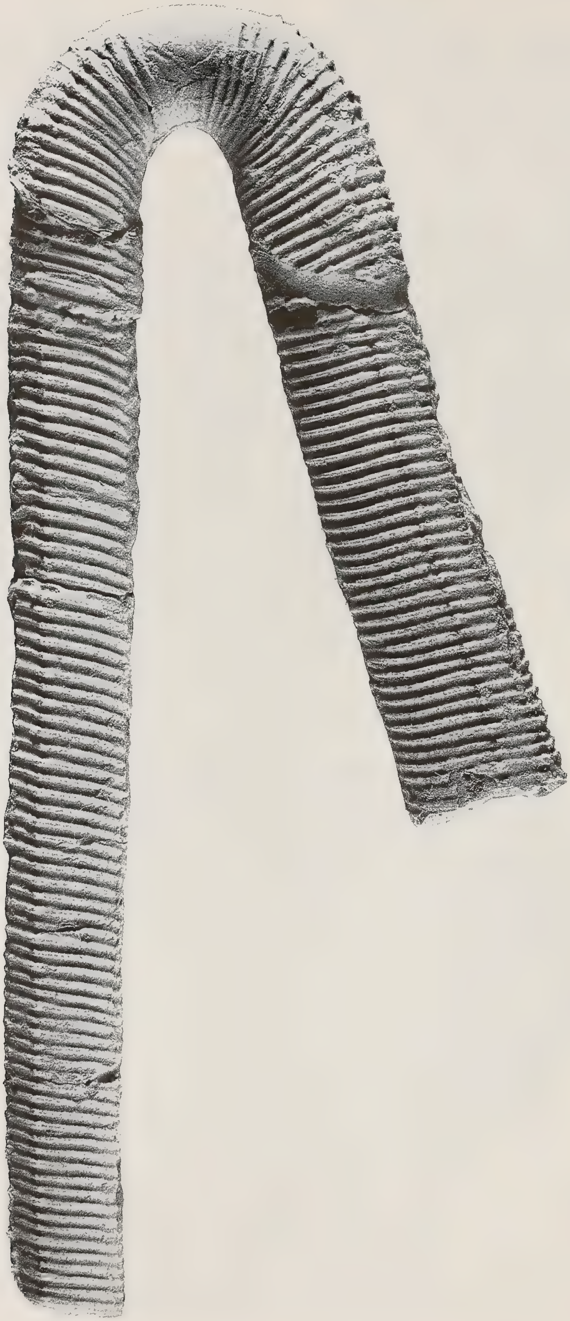

Figure 62

Pseudoxybeloceras (Pseudoxybeloceras) quadrinodosum (Jimbo, 1894). SAM–PCP18744 (ex Cape of Good Hope Geological Commission collection). From an unspecified horizon at the type section of the Mzamba Formation at the Mzamba River Estuary, Eastern Cape Province, locality 1, upper Santonian or lower Campanian. × 0.7.

Type

Lectotype by subsequent designation of Wright & Matsumoto (1954: 120) is the specimen figured by Jimbo (1894, pl. 7 (fig. 3)), housed in the collections of the University Museum, University of Tokyo, nr MM7524–1 from the Santonian?–Campanian of the Chiptanshibets on the Tumbets River, Kitami Province, Hokkaido.

Material

SAM–PCP18744 and SAM–P1411, both from an unspecified horizon at locality 1, the type section of the Mzamba Formation at the Mzamba River Estuary, Pondoland, Eastern Cape Province, Mzamba Formation, probably Santonian III.

Description

The larger of the two specimens, SAM–PCP18744 (Fig. 62), consists of two straight shafts, connected by an open U-bend, such that they are not strictly parallel, but slightly divergent. This appears to be the specimen from the Geological Survey, Cape Town, mentioned by Spath (1921*b*: 51) and refigured by Cooper (1994, fig. 2).

The whorl section is oval, higher than wide, with a rounded dorsum and flanks, but flattened in the intertubercular area over the venter and the ventrolateral third. Maximum width is at mid-flank. Ornament consists of fine, single ribs, each bearing four rows of small, pointed tubercles; one pair on the venter and the other at the ventrolateral third of the flanks. Ribbing on both shafts is prorsiradiate, but the degree of inclination and density varies slightly. At the smaller end there are 9 distinctly prorsiradiate ribs per whorl height; at the biggest end there are nearly 12 rectiradiate ribs per whorl height. Towards, and in the bend, ribbing changes from rectiradiate to rursiradiate.

The smaller specimen, SAM–P1411 (Fig. 60D), is slightly curved, and shows irregular development of the ventrolateral row of tubercles. These only occur on alternate ribs and are irregularly displaced on either side.

Discussion

The smaller specimen (Fig. 60D) was originally identified as *Pseudoxybeloceras*? sp. A by Klinger (1976: 77) because of the irregular tuberculation. However, seen in association with the adult specimen, it seems that this feature is merely part of the juvenile ornamentation. In the most comprehensive discussion of *P. (P.) quadrinodosum* so far, Matsumoto (1977: 345–347) also describes the early ornament. Here, however, the bituberculate stage passes directly to the quadrituberculate stage without intermediary bituberculate ribs as in the Pondoland specimen. The early stages of *P. (P.) quadrinodosum* thus show a combination of *Parasolenoceras* (type species *Parasolenoceras splendens* Collignon 1969: 44, pl. 530 (fig. 2087)) and *Christophoceras* (type species *Christophoceras ramboulai* Collignon 1969: 47, pl. 531 (fig. 2093)) features and further support our view that these could be included as subgenera of *Pseudoxybeloceras*; as also suggested by Matsumoto & Morozumi (1980: 19) and tentatively by Ward & Mallory (1977: 611) (as *Cyphoceras* Ward & Mallory, 1977) and most recently by Wright (1997: 253).

Hamites amapondensis Van Hoepen (1921: 15, pl. 3 (figs 5–6), text-fig. 9) is a clear

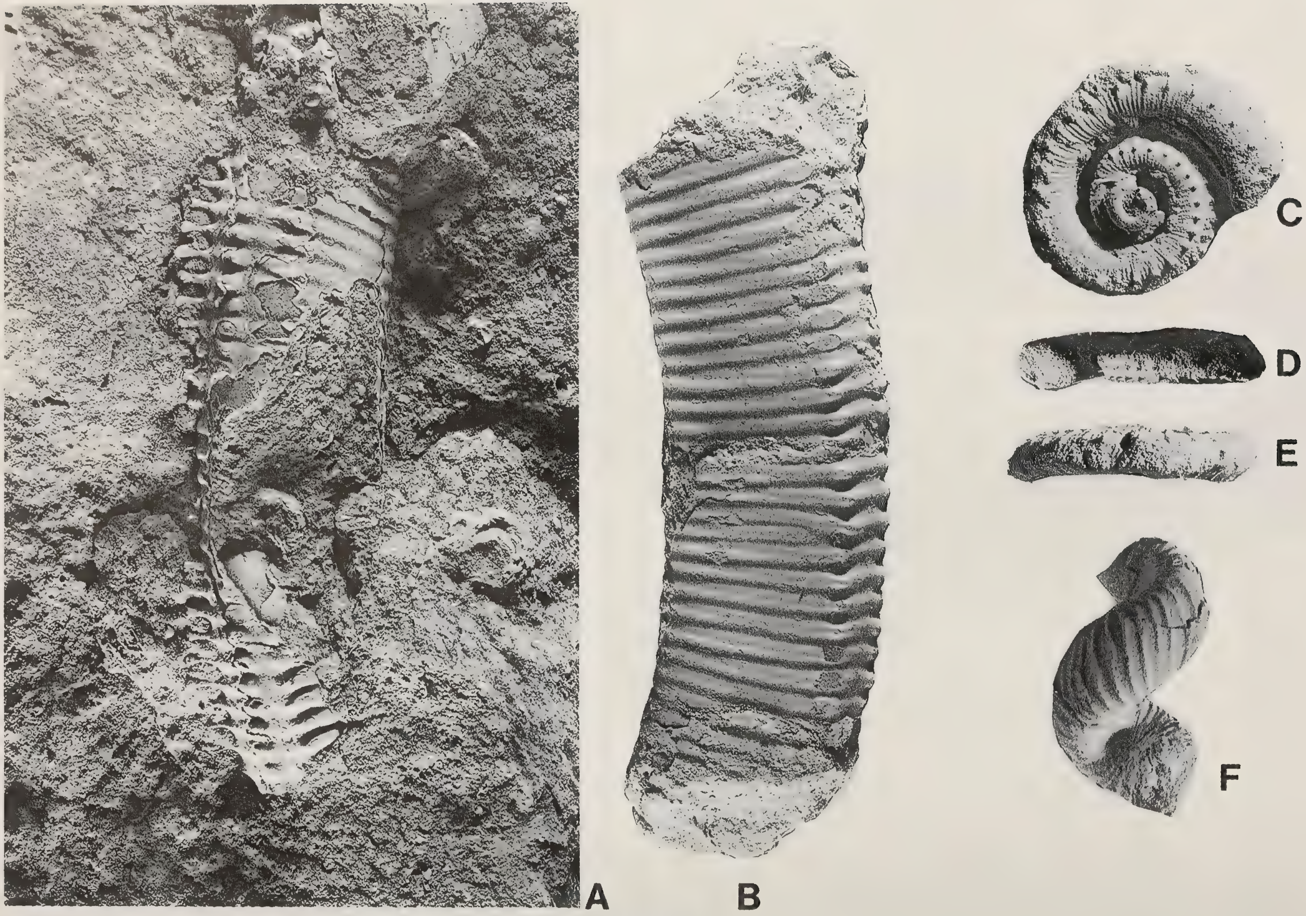

Figure 63

synonym of *P. (P.) quadrinodosum*, as Van Hoepen (1921: 16) had tentatively suggested. Differences quoted by him, e.g. details of the suture line, rib density and whorl section are all within the limits of intraspecific and ontogenetic variation.

Oxybeloceras? cf. *quadrinodosum* in Spath (1921*b*: 50, pl. 7 (fig. 2a–b)) with ventral tubercles only, is merely a juvenile of *P. quadrinodosum* as shown by the descriptions of Matsumoto (1977).

Occurrence

So far none of the Pondoland specimens have been accurately localized, but they probably occur in the upper Santonian. In Romania, Szasz (1974, 1982) records the species from the upper Campanian. The Japanese specimens are probably of Santonian age, but could be Campanian (Matsumoto 1977: 346). This seems to indicate a Santonian to Campanian age for the species in Japan, Romania and Pondoland.

Pseudoxybeloceras (Pseudoxybeloceras) matsumotoi Collignon, 1965
Fig. 63A–B

1965	*Pseudoxybeloceras matsumotoi* Collignon, p. 12, pl. 419 (fig. 1731).
1965	*Diplomoceras (Glyptoxoceras) subcompressum* Forbes; Collignon, p. 13, pl. 419 (fig. 1732).
1976	*Pseudoxybeloceras (Pseudoxybeloceras) matsumotoi* Collignon; Klinger, p. 76, pl. 33 (fig. 6).
2003	*Pseudoxybeloceras matsumotoi* Collignon; Klinger & Kennedy (This volume 110 (5)), p. 199, figs 1–10.

Type

Lectotype designated by Klinger & Kennedy (2003: 214) is the specimen figured in Collignon (1965, pl. 419 (fig. 1731)) GD11731 from the lower or middle Coniacian of Beantaly (Belo sur Tsiribihina), Madagascar.

Material

SAM–PCZ18747 (ex SAS–92/1) from bed 1 at locality 92, KwaZulu, St Lucia

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Fig. 63 (*see facing page*). A–B. *Pseudoxybeloceras (Pseudoxybeloceras) matsumotoi* Collignon, 1965. A. SAM–PCZ18747 (ex 92/1) from locality 92, KwaZulu, St Lucia Formation, Coniacian II. Note the distinct spatulate endings of the spines. B. NMB–PCZ18743 from locality 145, KwaZulu, St Lucia Formation, Coniacian II. C–E. *Neocrioceras (Schlueterella) compressum* Klinger, 1976. Natal Museum, Durban collections, the original of Spath's (1921*b*: 52, pl. 7 (Figs 6a–c)) *Neocrioceras* cf. *spinigerum*, and the 'genotype' of *Neocrioceras sensu* Spath (1921*b*: 51) from an unspecified horizon at the type locality of the Mzamba Formation, Mzamba River Estuary, Eastern Cape Province, locality 1, upper Santonian or lower Campanian. F. *Eubostrychoceras (Eubostrychoceras) zulu* sp. nov. SAM–PCZ18709, a paratype from locality 72, St Lucia Formation, Coniacian II. A–E × 1; F × 2.

Formation, Coniacian II; NMB–PCZ18743 from locality 145, KwaZulu, St Lucia Formation, Coniacian II.

Description

The specimen originally figured by Klinger (1976, pl. 33 (fig. 6)) is here refigured (Fig. 63A) to show the spatulate shape of the hollow spines, where preserved. The other specimen, NMB–PCZ18743 (Fig. 63B) is virtually identical to the lectotype. The whorl section is elliptical (Wb:Wh = 21.5:30.4 (0.71)). Ornament consists of predominantly single, radial ribs, numbering about 8 or 9 per whorl height. Each bears a small pair of ventrolateral, radially elongated tubercles and a larger pair of ventral tubercles. As mentioned above, in shelly preservation these bear long, spatulate, hollow spines.

Discussion

Hollow spines are rarely preserved in heteromorphs. These may be quite variable, but are generally pointed and sealed off from the rest of the shell by a convex septum. Spatulate spines that are somewhat similar to those of *P. (P.) matsumotoi* have been observed in *Hyphantoceras (H.) reussianum* (see e.g. Metzdorf 1992, pl. 1 (figs 7–8)) and *P. (P.)* aff. *lineatum* (*In:* Olivero 1988, fig. 3C–D).

A full discussion of the ontogeny, shell structure and differential preservation of internal moulds of the phragmocone and body chamber respectively in *P. matsumotoi* is given by Klinger & Kennedy (This volume 110 (5)).

Occurrence

Rare in Coniacian II of KwaZulu, common in the lower and middle Coniacian of Madagascar.

Genus *Spiroxybeloceras* Kennedy & Cobban, 1999

Type species

Ptychoceras meekanum Whitfield, 1877: 44, illustrated by Whitfield 1880, pl. 16 (figs 1–2) from the Pierre Shale, Wyoming, by original designation of Kennedy & Cobban (1999: 74).

Diagnosis

Early stage loose, planispiral, followed by two parallel shafts barely in contact. Ornament consists of narrow, sharp ribs that bear small pointed tubercles on the venter.

Discussion

There is some confusion about the validity of three genera with very similar adult stages: *Solenoceras* Conrad, 1860 (type species *Hamites annulifer* Morton, 1841: 109), *Oxybeloceras* Hyatt, 1900 (type species *Ptychoceras crassum* Whitfield, 1880: 459) and *Spiroxybeloceras* Kennedy & Cobban, 1999 (type species *Ptychoceras meekanum* Whitfield, 1877). According to Kennedy & Cobban (1993*a*: 142), *Solenoceras* and

Oxybeloceras differ in that: (1) '*Solenoceras* consists of two straight parallel shafts, lacking the initial planispire of *Oxybeloceras*'; (2) *Solenoceras* has 'the shafts closely adpressed for all their length'; (3) 'constrictions with associated flared ribs occur on the body chamber and phragmocone'; (4) 'The ribs bearing tubercles are weaker than in *Oxybeloceras* and the tubercles may efface'.

Spiroxybeloceras is similar to *Solenoceras*, but differs in having an early ontogenetic stage consisting of a loose planispiral growth stage, followed by two parallel shafts barely in contact. *Solenoceras*, in contrast, has an early ontogenetic stage consisting of an ammonitella, followed by a straight shaft which is impressed in a second, parallel shaft.

Occurrence

Solenoceras s.l. occurs in the upper Campanian and lower Maastrichtian, and has been recorded from the Gulf Coast regions of the USA, Angola, Nigeria, Egypt, the Middle East, Spain, Madagascar, KwaZulu and Japan.

Spiroxybeloceras minimus (Basse, 1931)

Fig. 64

1931 *Hamites (Ptychoceras) minimus* Basse, p. 17, pl. 1 (figs 20–22).
?1931 *Hamites (Ptychoceras)* cf. *Humei* Douvillé; Basse, p. 18, pl. 6 (figs 9–10).
1976 *Solenoceras* sp. cf. *texanum* (Shumard); Klinger, p. 77, pl. 34 (fig. 7).

Type

Lectotype here designated is the specimen figured by Basse (1931, pl. 1 (figs 20–22)) from Andrafiavelo, Madagascar.

Material

SAM–PCZ17365 (ex SAS–A2083), probably from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b. SAM–PCZ7899, SAM–PCZ7900a, b, SAM–PCZ18745–6, SAM–PCZ9890, all from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b.

Description

The new material shows the early criocone whorls of the species. Unfortunately these are only preserved as imprints or incomplete secondary infillings. The rest of the shell consists of two slightly curved shafts. The smaller is distinctly impressed into the dorsum of the larger. Ornament consists of fine, sharp-crested ribs. In the curved section connecting the two shafts, the ribs are interrupted over the venter and end in a pair of small ventrolateral tubercles. On the rest of the shell, the ribs are continuous over the venter. Minute tubercles can be seen under oblique lighting on the body chamber shaft.

The species is very small—the total length of the final shaft is 30 mm or less. The mode of occurrence of the material is of interest. One of the specimens, SAM–PCZ7899 is situated in part of the body chamber of *Nostoceras (Bostrychoceras) sanctaeluciense*. In the nodule SAM–PCZ18745–6, at least seven specimens are visible.

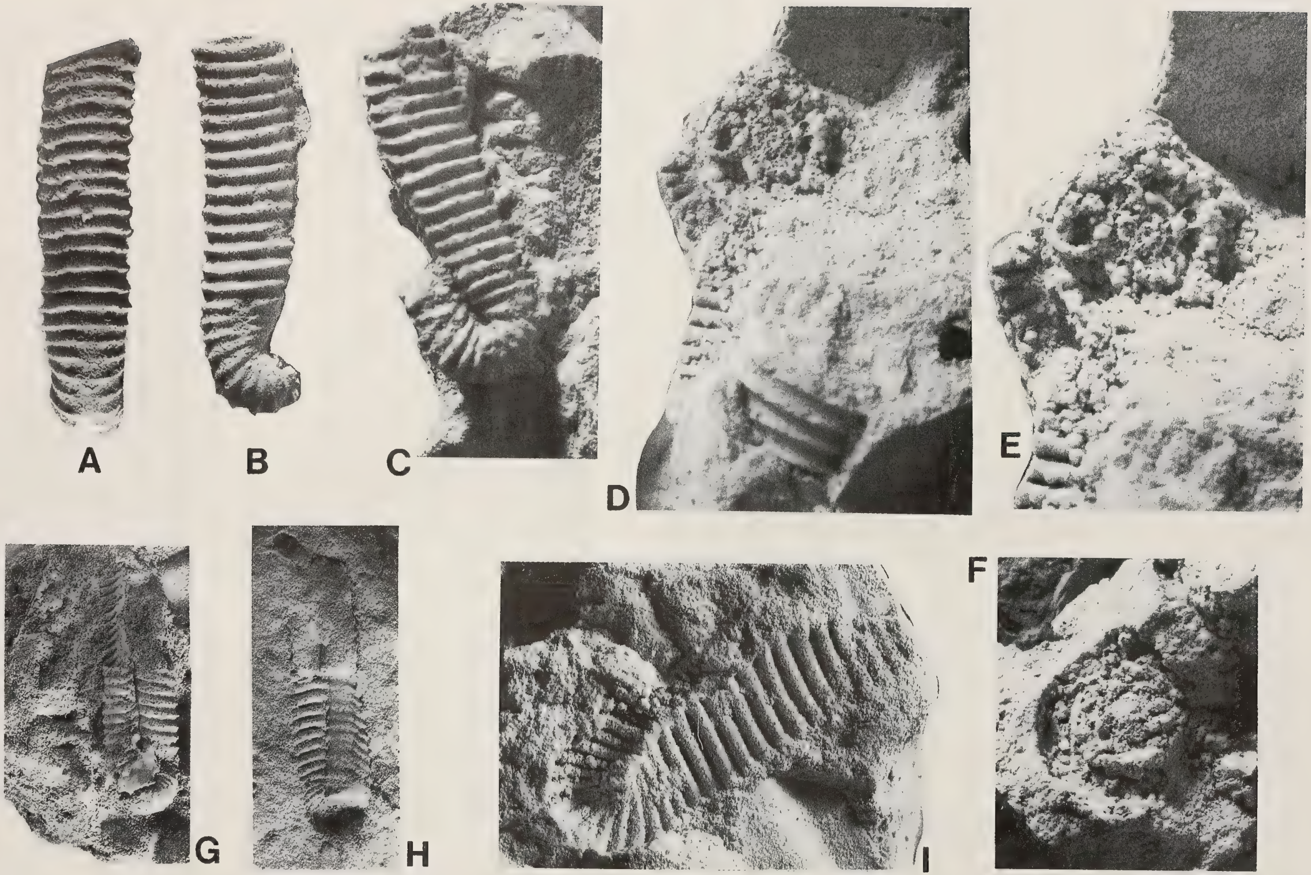

Figure 64

Spiroxybeloceras minimus (Basse, 1931). A–B. SAM–PCZ7900a. C. SAM–PCZ9890. D–F. SAM– PCZ18745. G. SAM–PCZ17365 (ex A2083). H. SAM–PCZ7900b. I. SAM–PCZ18746. All from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b. Note the open, criocone early whorls in D–F. A–C, I × 2; G–H × 1; D–F × 4.

Discussion

The presence of early criocone whorls, first suggested by Whitfield (1892: 273) and substantiated by Lewy (1967: 170, pl. 3 (figs 1–2)) in *Spiroxybeloceras humei humei* (Douvillé, 1929) is further confirmed by the present material.

Klinger (1976: 77) initially identified a single specimen of this genus as *Solenoceras* sp. cf. *texanum* and distinguished it from *S. minimus* (Basse, 1931) on account of the denser ribbing of the latter. Basse's figures (1931, pl. 1 (fig. 20–22)) show very fine tubercles on the final shaft, similar to those in SAM–PCZ7900a. The small size, the impression of the first shaft into the dorsum of the second, and the very fine ventral tuberculation on the final shaft are characteristic of the species.

It is difficult to separate all known species of *Spiroxybeloceras* satisfactorily. Perhaps because of their small size, individuals are not very common in collections. In addition, complete specimens are rare. *S. texanum* (Shumard) (1861: 190) (see Stephenson 1941: 399, pl. 77 (figs 4–5), pl. 79 (figs 1–4)) with which our KwaZulu material had previously been tentatively identified, has very distinct ventral tubercles and is easily separated.

Occurrence

Lower Maastrichtian, Madagascar and KwaZulu.

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6. SYSTEMATIC papers must conform to the International code of zoological nomenclature (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc. The name of the taxon should be followed, without intervening punctuation, by the author's(s') name(s) (not abbreviated) and the year of publication; a comma must separate author's(s') name(s) and year. The author's(s') name(s) and date must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be either according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order (see example 1), or according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry (see example 2). The author should adopt one style or the other throughout a paper.

Family **Nuculanidae**
Nuculana (Lembulus) bicuspidata (Gould, 1845)
Figs 14–15A

Example 1
Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata (Gould) Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871, pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata (Gould): Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

NOTE punctuation in the above example: comma separates author's name and year; semicolon separates more than one reference by the same author; full stop separates references by different authors; figures of plates are enclosed in parentheses to distinguish them from text-figures; dash, not comma, separates consecutive numbers.

Example 2
1845 *Nucula (Leda) bicuspidata* Gould, p. 37.
1856 *Leda plicifera* A. Adams, p. 50.
1859 *Laeda bicuspidata* (Gould) Hanley, p. 118, pl. 228 (fig. 73).
1861 *Nucula largillierti* Philippi, p. 87.
1871 *Laeda bicuspidata* (Gould): Sowerby, pl. 2 (fig. 8a–b).
1950 *Leda bicuspidata* (Gould): Nicklès, p. 163, fig. 301.
1955 *Leda bicuspidata* (Gould): Nicklès, p. 110.
1964 *Leda bicuspidata* (Gould): Barnard, p. 234, figs 8–9.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated allotype (if applicable) and/or paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype. SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33 51 S25 39 E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text, e.g. '… the Figure depicting *C. namacolus* …', or '… in *C. namacolus* (Fig. 10) ….'

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     NOTE: no comma separating name and year; pagination indicated by colon, not p. (except in synonymies, see example 2); names of joint authors connected by ampersand; *et al.* in text for more than two joint authors, but names of all authors given in list of references.
   - (b) Full references at the end of the paper, arranged alphabetically by names, chronologically within each name, with suffixes *a*, *b*, etc., to the year for more than one paper by the same author in that year, e.g. Smith (1969*a*, 1969*b*) and not Smith (1969, 1969*a*).

     For books give title in italics, edition, volume number, place of publication, publisher.

     For journal articles give title of article, title of journal in italics (according to the World list of scientific periodicals. 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number in parentheses (if pagination discontinuous), pagination (first and last pages of article).

     Examples (note capitalization and punctuation)

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     FISCHER, P. H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* **74**: 627–634.

     KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) **2**: 309–320.

     KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* **17** (4): 1–51.

     THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungreise im westlichen und zentralen Süd Afrika ausgeführt in den Jahren 1903–1905* **4** (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* **16**: 269–270.

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ANNALS OF THE SOUTH AFRICAN MUSEUM

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Volume **111** Band
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Part 1 Deel

BASKETWORK OF SOUTHERN AFRICA.
PART 3

BASKETWORK OF THE SOUTHERN NGUNI

by

E.M. SHAW

The South African Museum forms part of Iziko Museums of Cape Town

The Annals of the South African Museum publishes original research articles, revisions and review articles in natural history (palaeontology, geology, entomology, herpetology, ornithology, mammalogy, and marine and freshwater biology), social history (anthropology, archaeology and history), and art.

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BASKETWORK OF SOUTHERN AFRICA
PART 3

BASKETWORK OF THE SOUTHERN NGUNI

by
E. M. SHAW†
*formerly of the South African Museum,
Iziko Museums of Cape Town*

(With 52 figures)

[*MS accepted February 1995*]

ABSTRACT

In Part 1 of this study, the techniques and materials used in southern African basketwork were described (Shaw 1992). Part 3 continues the ethnographic part of the study and describes the basketwork of the people of the Eastern Cape Province, who are the southernmost branch of the Nguni-speaking people. In addition to the various group affinities, two divisions can be distinguished: the earliest entrants into the area, and other later immigrants from KwaZulu-Natal.

The Southern Nguni used basketwork for many purposes. They also traded baskets to neighbours, and some of the early examples now in museums were collected from the Gonaqua (Khoekhoe) who had obtained them from the Xhosa. The increasing availability of first metal and then plastic alternatives caused the disappearance of the early watertight baskets, which were difficult and slow to make. Although some uses or objects made have disappeared, as is shown by the terms recorded earlier but no longer current, the craft was still vigorous in the 1960s and 1970s in some places when the fieldwork was undertaken, especially in the making of gifts for special occasions, such as weddings. There are some local differences, and indications are that at one time these were more marked and demonstrated distinct traditions of basketry.

EDITORIAL NOTE

E. M. Shaw began research for this project on the basketwork of southern Africa in the middle of the last century, and continued to gather and process data until the 1990s. Two volumes were published (1992 and 1993), and this volume was in the final stages of preparation when Miss Shaw died in 2002. As colleagues we were asked to check and correct the MS before submission for publication. Obvious anomalies were corrected, such as the adoption of the term Khoekhoe for Khoikhoi or Hottentot. Botanical terms quoted by Miss Shaw in the text have been retained. Contemporary names for provinces have been adopted, but descriptive regional names like Mpondoland have been retained. Elsewhere, attempts were made to discern and respect Miss Shaw's wishes regarding the use of other obsolete terminology for historical accuracy.

Ann. S. Afr. Mus. **111** (1), 2004: 1–78, 52 figs.

One reviewer of the manuscript congratulated Miss Shaw on '… a most useful and painstakingly executed piece of research and synthesis. Not many ethnographers (a rare breed, alas) would have had the patience to carry out such a task …'. Miss Shaw's highly specialized knowledge of the technology of basketwork is reflected in the presentation of the information. We had difficulties resolving certain problems, such as the linking of some technical illustrations to the text, without this knowledge. Readers with a special interest in basketwork technology are referred to her earlier volumes.

This publication, the last in a distinguished series on material culture by E. M. Shaw, will provide a reference point in the study of indigenous knowledge systems in South Africa. Interest in the relationships between people, their environment, and their material culture, continues to inform museum collections and provides the impetus for future research and interpretation.

The final technical editing was done by Ms J. Friedlander.

Gerald Klinghardt
Lindsay Hooper

Social History Collections Division
Iziko Museums of Cape Town
February 2003

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INTRODUCTION

The Eastern Cape and neighbouring areas have been the home for several centuries firstly of Thembu, Xhosa, Bomvana, Mpondomise and Mpondo, Vundla of Quthing and Umzimkulu, and Nci of Harding and Umzimkulu. According to tradition they entered the area from the north-east and moved gradually south and westward, and in the case of the Vundla, north again. As far as is known at present, they were the first Ntu-speaking people to enter the area.

As a result of increasing pressures in KwaZulu-Natal, they were followed in the east at various times by Xesibe, Bhaca, Xolo, Nzimakwe and Nhlangwini, and finally by Hlubi and Mfengu, who were direct fugitives from the Zulu wars of the early nineteenth century.

Together these are the southern branch of the Nguni-speakers. Xhosa is now the language spoken throughout, with some differences of dialect. It should be noted that, through dialectical differences (and individual's terms) in different parts of the Eastern Cape, two objects that are apparently the same may, in their respective areas, have different names and/or uses and, conversely, the same name may be applied to objects having different purposes.

Part 1 of this series dealt with the technology of the basketwork (Shaw 1992). Individual named techniques were given numbers (e.g. chequer weave, *1a*). The same numbering system is followed here in the captions to Figures 1–3.

As in Part 2 Basketwork of the Khoisan and Dama (Shaw 1993), the text is arranged under headings of class of basket or other object, and the authors are quoted in date order of sojourn and grouped as Early – up to 1899, and Recent – from 1900. Examples from both time periods were seen and examined. Most of the information was obtained from fieldwork, which was undertaken by the author at intervals between 1948 and 1971, and fieldwork undertaken by South African Museum colleagues, P. Davison and L. Hooper, between 1984 and 1986. Records relating to fieldwork are listed as 'Field survey'. Many museum collections were examined in southern Africa and in Europe. Over 400 examples were examined and noted and more observed in the field.

TECHNIQUES

The techniques used by the Southern Nguni are shown in Figures 1–3.

Figure 1. A–Z. FABRIC. AA–LL. BEGINNINGS.

A–K (*page 5*). A. Straight chequer weave, *1a*. B. Diagonal twill, *2b*. C. Plain wrapped weave, *3*. D. Lattice wrapped weave, *3*. E. Plain close twined weave, single warp, *4a*. F. Plain close twined weave, multiple warp, *4b*. G. Plain open twined weave, single warp, *4c*. H. Plain open twined weave, multiple warp, *4d*. I. Close chain twine over multiple warp, *4f*. J. Twilled twine, *4g*. K. Close zigzag split-warp twine, *4h*.

L–W (*page 6*). L. Open zigzag split-warp twine, *4i*. M. Close diagonal split-warp twine, *4j*. N. Open diagonal split-warp twine, *4k*. O. Chequer wicker, *5a*. P. Chequer wattlework, *6a*. Q. Simple plait, *7a*. R. Round plait, *7o*. S. Square plait, *7q*. T. Several stranded spiral plait, *7t*. U. Straight sewing, single foundation, *8*. V. Straight sewing, twisted composite foundation, *9a*. W. Straight sewing, flat coiled plaited foundation, *10a*.

X–LL (*page 7*). X. Simple sewing over coiled multiple foundation, *11b*. Y. Plain beeskep sewing over coiled multiple foundation, *17a*. Z. Close furcate sewing twice into one hole, over coiled multiple foundation, *18c*. AA. Warps side by side, joined by first row of weft, *20a*. BB. Elements knotted in pairs for twilled work, *25*. CC. Elements knotted one end; end of sewing strand knotted, *29a*. DD. Bound warp, *31*. EE. Looped warp, *32*. FF. Twined weft for elliptical shape, *33b*. GG. Bent foundation for sewn work, *37a*. HH. Closed ring of foundation, *38a*. II. Open ring of foundation, *38b*. JJ. End of foundation knotted, *39*. KK. End of sewing knotted, *40*. LL. Double chequer square, *43a*.

Figure 2. A–D. SHAPING. E–U. EDGES – WARP OR FOUNDATION OF STRAIGHT SEWING. V–AA. EDGES – WEFT OR STRAIGHT SEWING. BB–EE. EDGES – COILED SEWN WORK.

A–I (*page 8*). A–D. Shaping. A. Pairing warps, *46b*. B. Adding warps, *47a*. C. Removing foundation strands in straight sewing, *48*. D. Placing of foundation coil, *51a*. E–U. Edges E. Front selvedge on diagonal twill, *67b*. F. Double selvedge on diagonal twill, *67c*. G. Bent warp selvedge on twine, multiple warps held by single row, *68a*. H. Scalloped selvedge on twine, multiple warp, front, back, front, and cut, *68c*. I. Scalloped selvedge on twine, part multiple warp up to edge, far side cut, *68e*.

J–T (*page 9*). J. Scalloped selvedge on twine, part multiple warp up to edge, near side cut *68d*. K. Scalloped selvedge on twine, weaving part warp up to edge before cut, *68h*. L. Scalloped selvedge on twine, warps front, back and under twining, *68n*. M. Plaited edge, full warp, *68p*. N. Plaited edge, part warps, *68q*. O. Edge of close twine on open twine, same direction, *75a*. P. Edge of close twine on any technique, opposite direction, *75b*. Q. Wrapped edge, *76a*. R. Wrapped edge, chain effect, *76j*. S. Knotted edge, *79a*. T. Knotted edge, fringe below knots, *79c*.

U–EE (*page 10*). U. Stapled edge on wicker or wattle, *80*. V. Weft threaded back on tracks to end off, *84d*. W. Weft continues straight back from edge, *85a*. X. Weft carried down tautly to next row, *85d*. Y. Weft back and forth and half-hitched between rows, *85i*. Z. Weft wound round last warp to next starting place, *85j*. AA. Wrapped edge, *86a*. BB. Plain blanket stitch, *95a*. CC. Oversewing over thinned last coil, *90*. DD. Herring-bone edge, *96a*. EE. Flat diagonal oversewing on top of coil, *97b*.

Figure 3. A–F. FINISHINGS. G–W. DECORATION. X–CC. ORNAMENTATION AND UTILITARIAN ADDITIONS.

A–J (*page 11*). A. Ends knotted separately, *106b*. B. Ends bound together in same direction to form a knob, *109a*. C. Ends laid together and half-hitched, *109d*. D. Spiny cone on straight sewing, *110b*. E. Elements turned inside and knotted, *114*. F. Knots turned in and sewn invisibly, *115a*. G. Band of different twine, *125a*. H. Twining in pattern between rows of open twine, *125b*. I. Bands of chain twine on plain twine, *125e*. J. Rows of lattice twine, *125g*.

K–S (*page 12*). K. Lines or patterns by lengthening stroke, *125j*. L. Raised line of three strand twine, *125k*. M. Extra strand introduced to make a chain pattern, *125n*. N. Rows of crossed warp in open twine, *125s*. O. Lengthening twists of composite foundation in straight sewing, *129b*. P. Change of direction of twists in straight sewing, *129d*. Q. Lengthening stitch in coiled sewing, *131*. R. Pattern by half-hitching sewing strand round neighbouring stitch, *134a*. S. Coloured pattern on twill in same material dyed, *143b*.

T–CC (*page 13*). T. Pattern on twine with two different coloured wefts, *145d*. U. On straight sewn, coloured foundation strand of same material dyed, *149a*. V. On coiled sewn, band of different coloured foundation, *150a*. W. On coiled sewn, different coloured sewing strand, *151a*. X. Sewn embroidery, *158d*. Y. Brass buttons and beads, *162, 163b*. Z. Lid, *164*. AA. Hanging strap, *165*. BB. Stiff cord handle on twilled bag, *166a*. CC. Stiff handle on sewn work, *167b*.

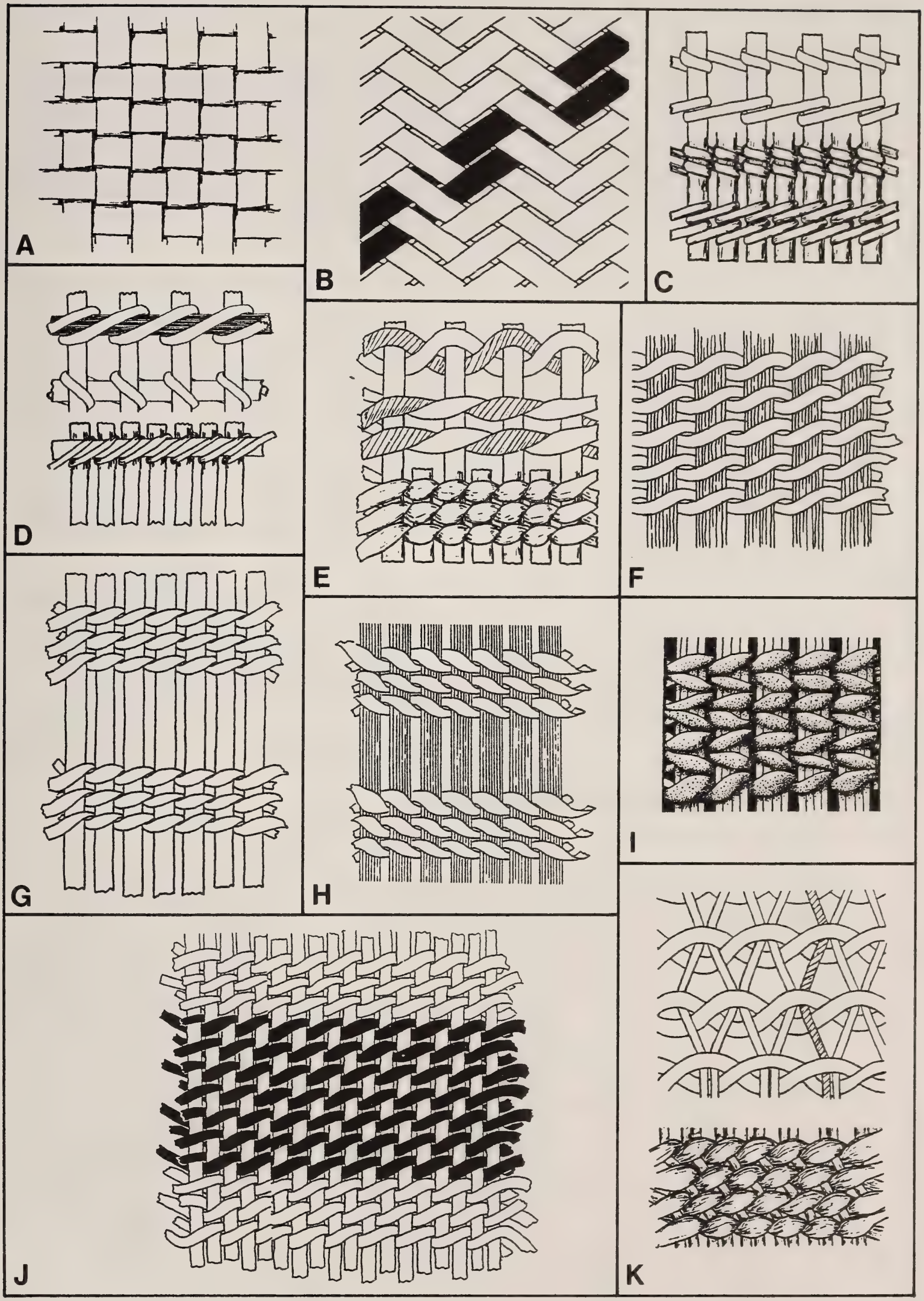


Figure 1A–K

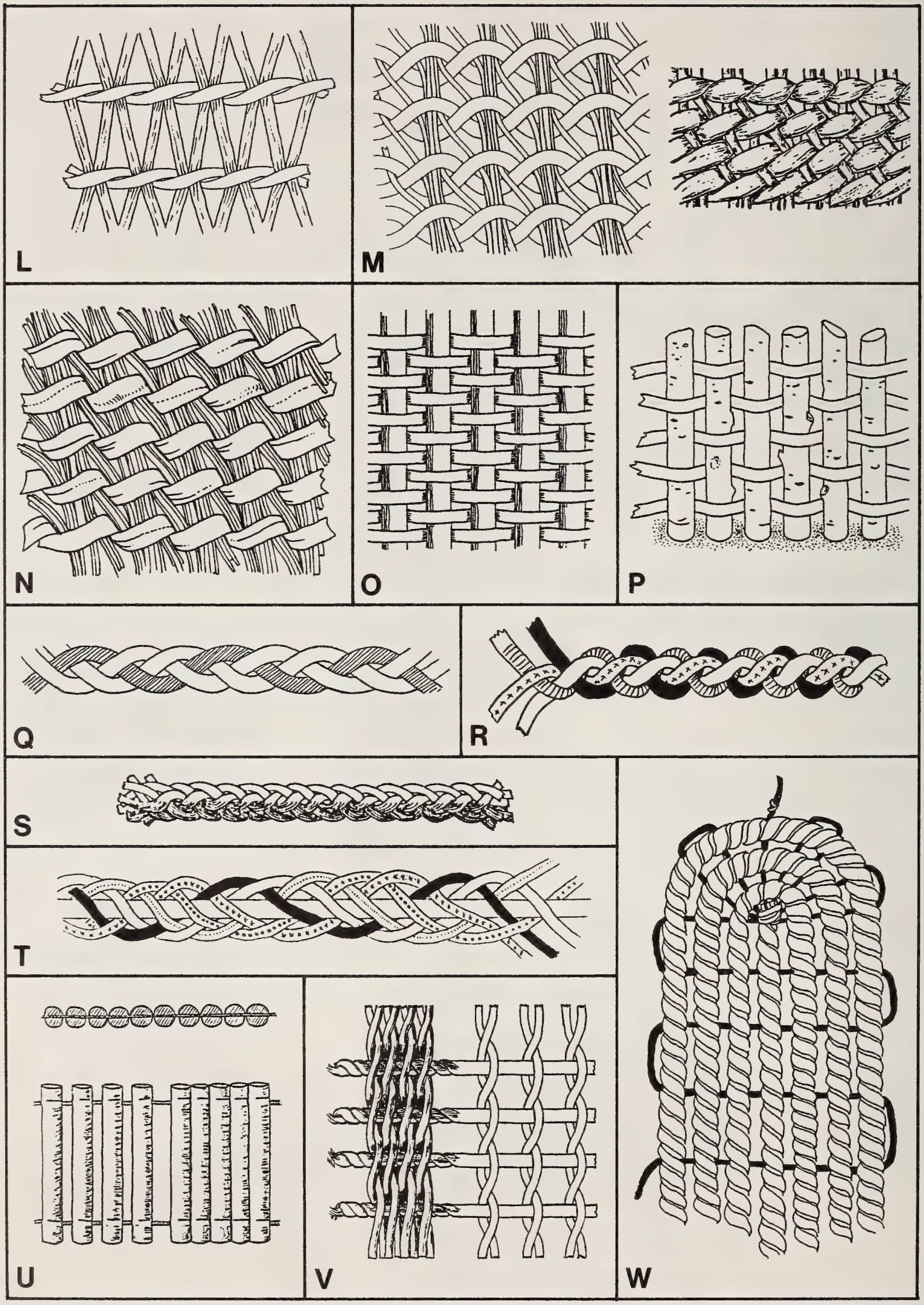


Figure 1L–W

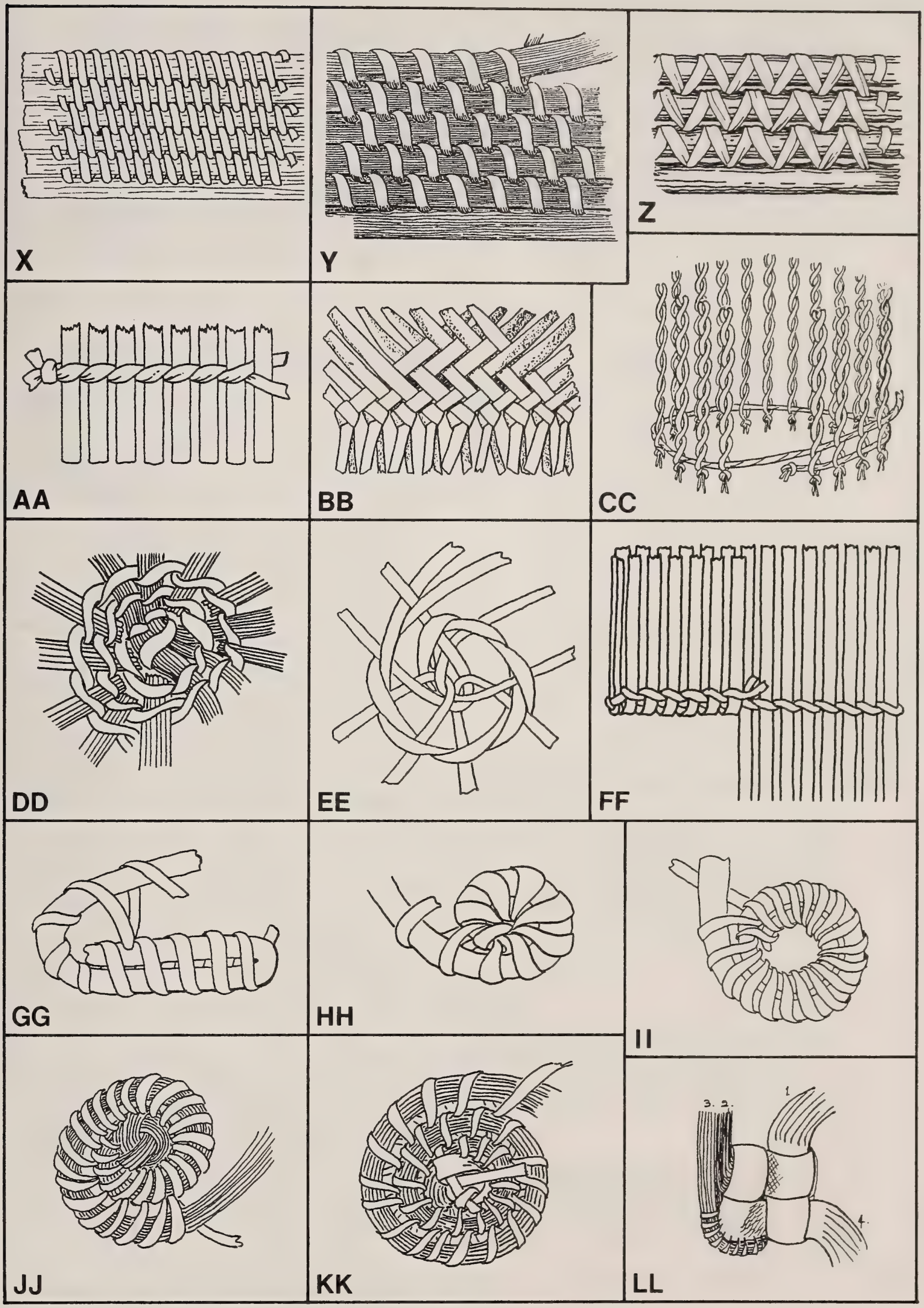


Figure 1X–LL

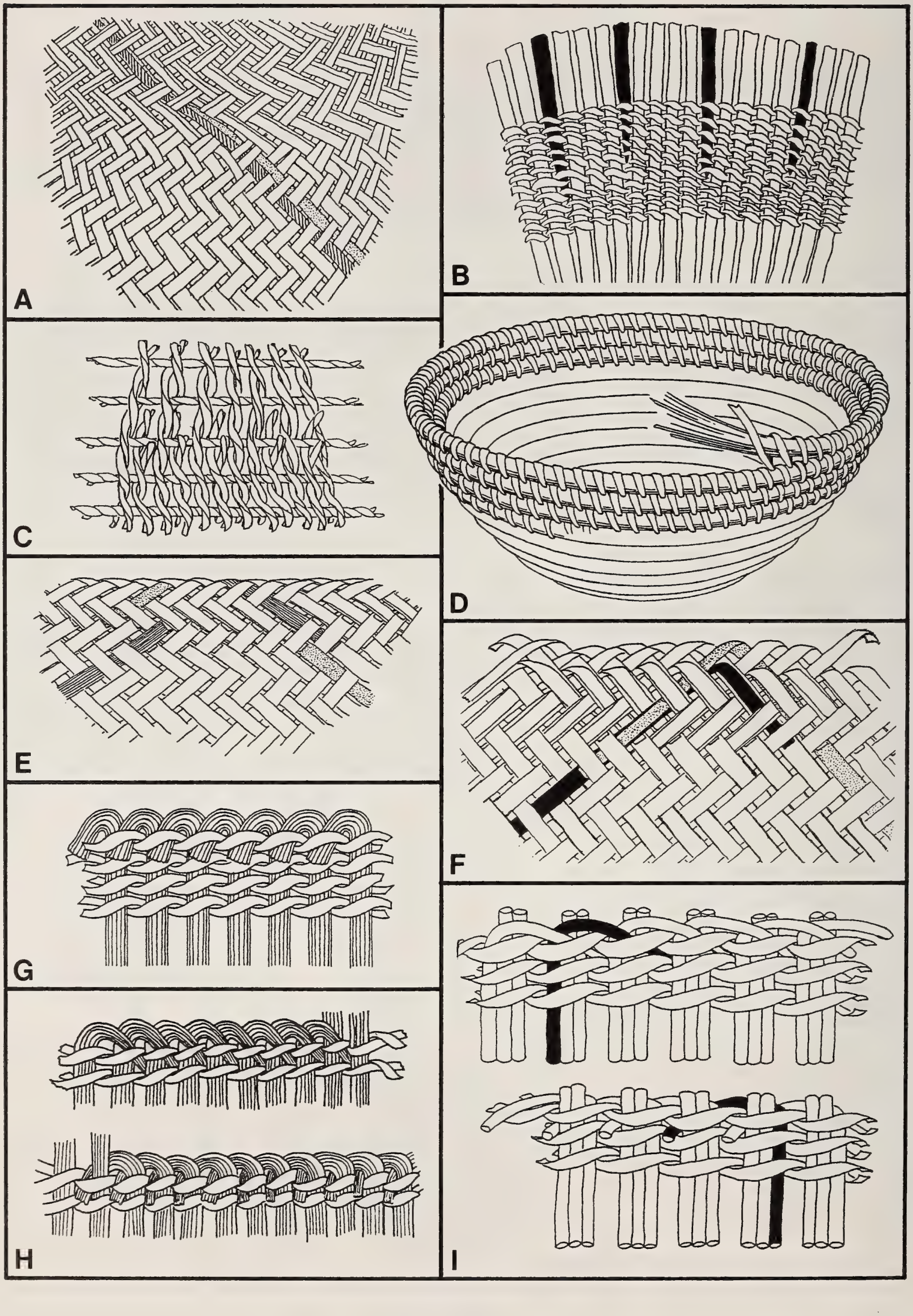


Figure 2A–I

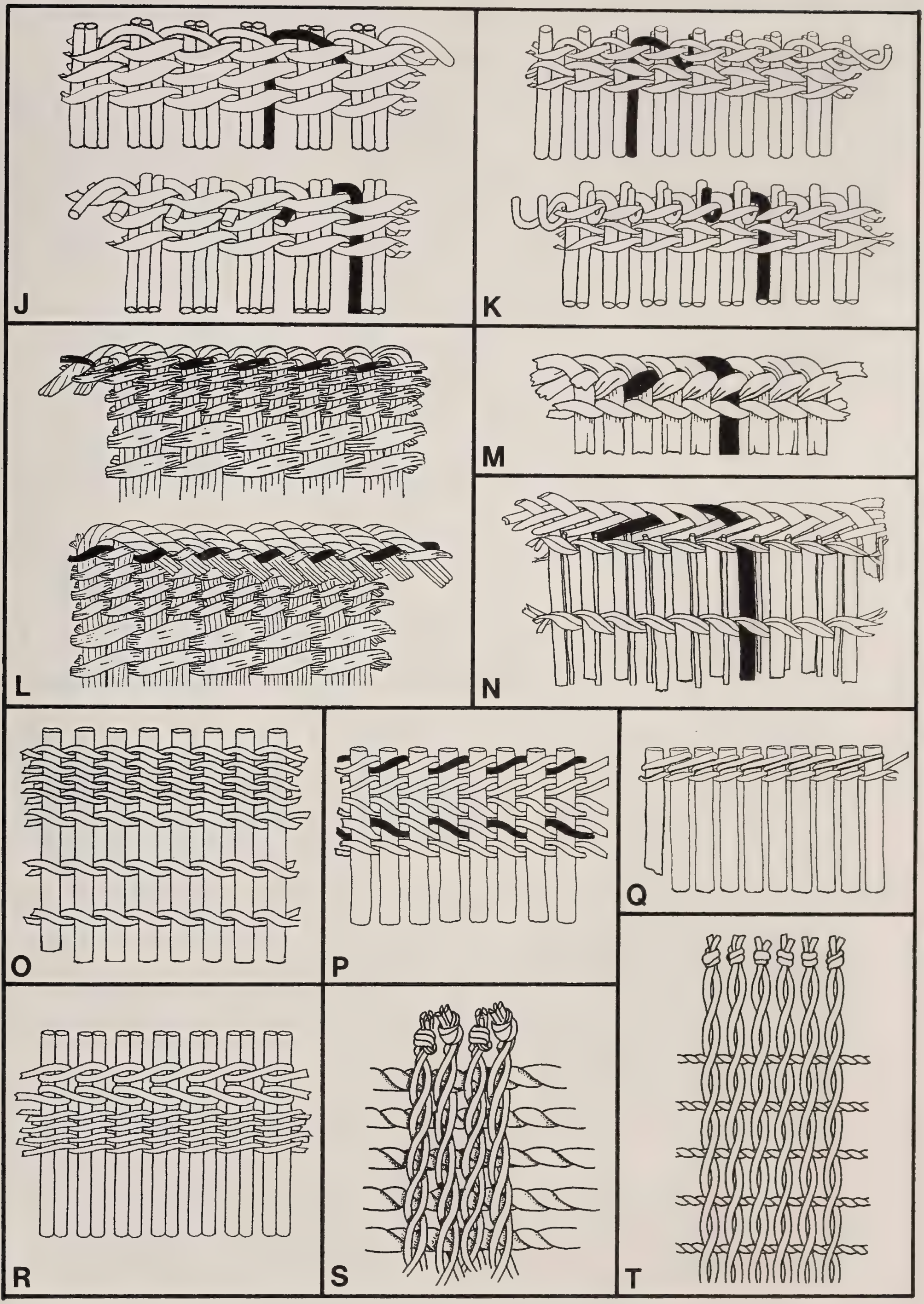


Figure 2J–T

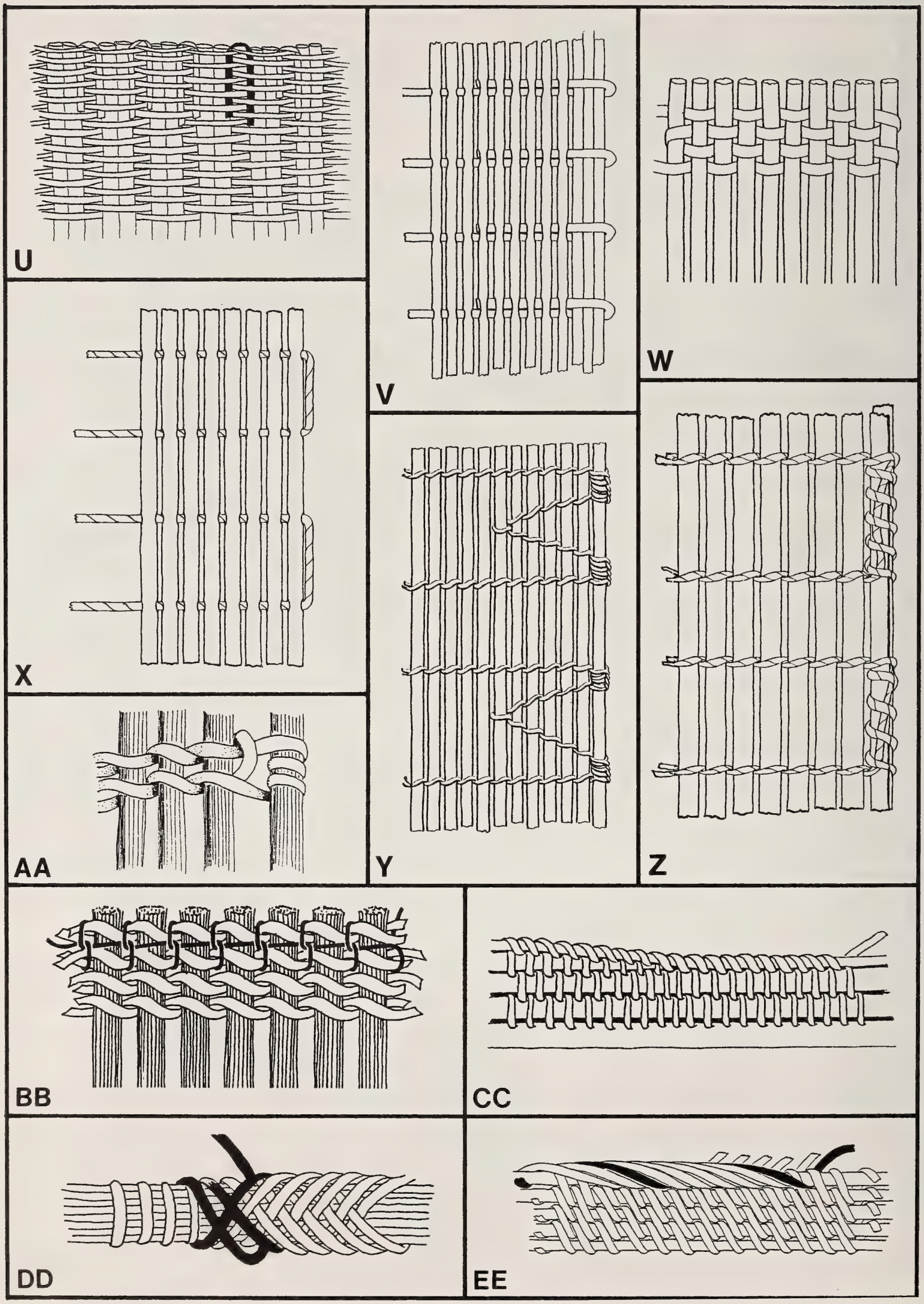


Figure 2U–EE

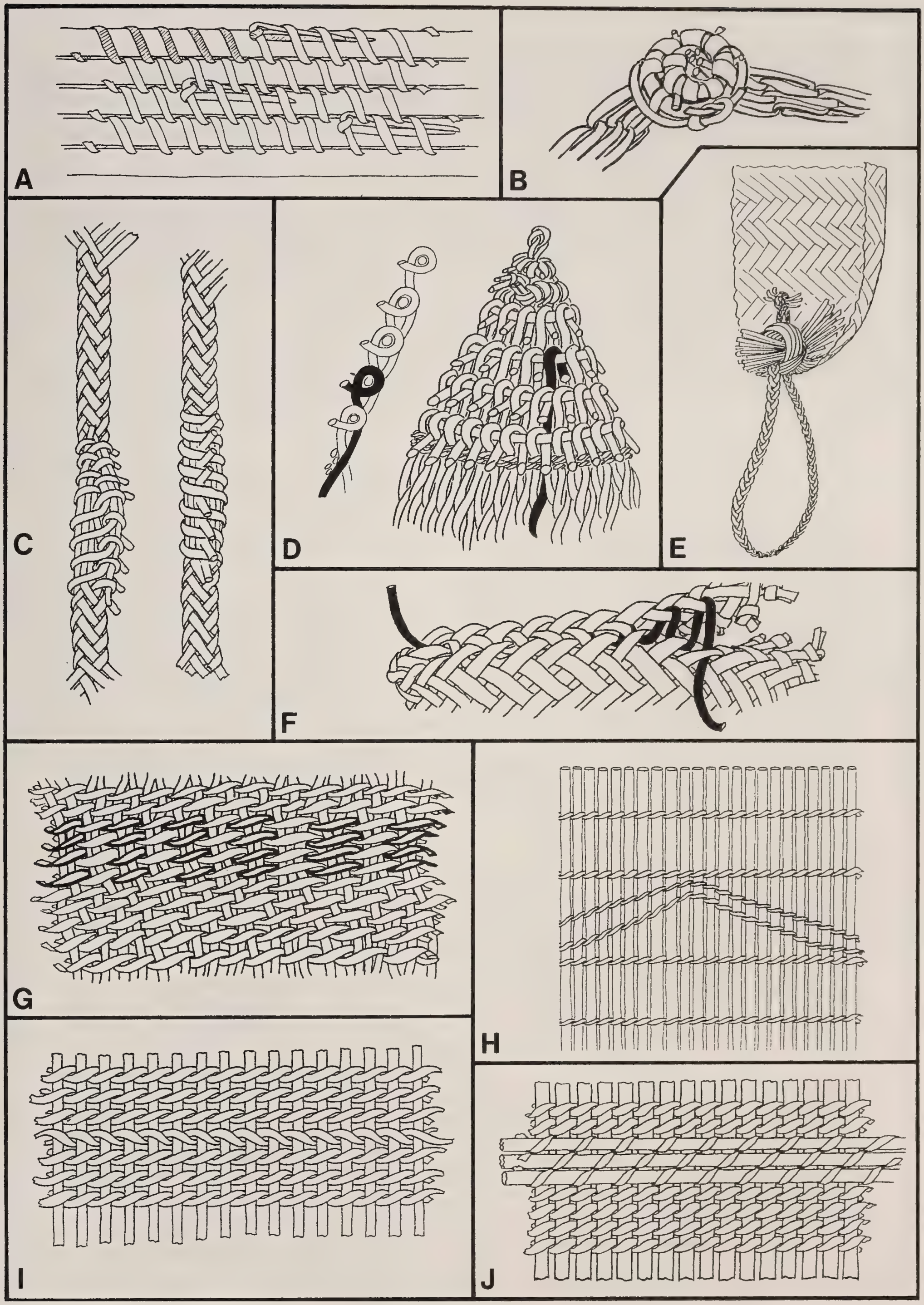


Figure 3A–J

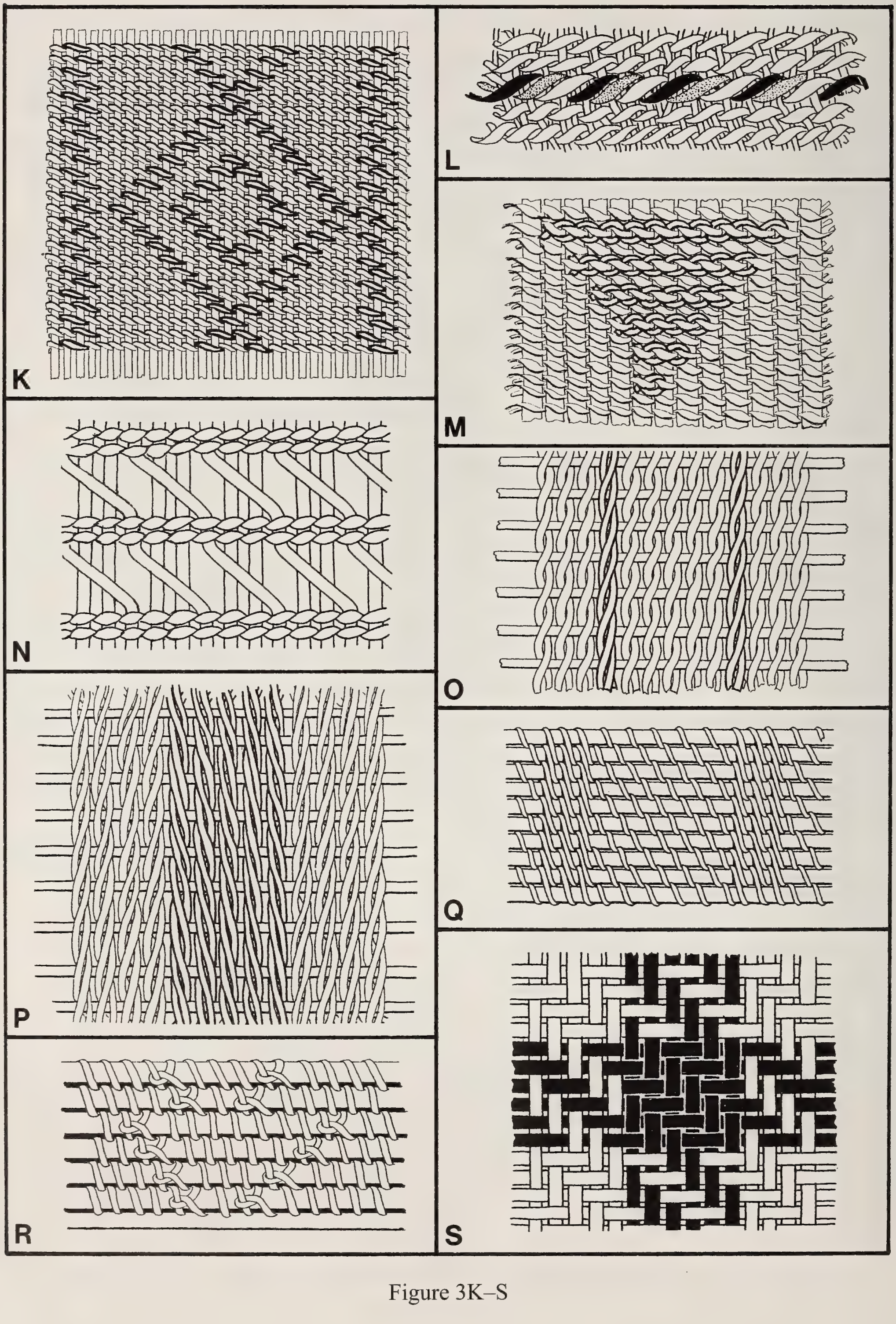


Figure 3K–S

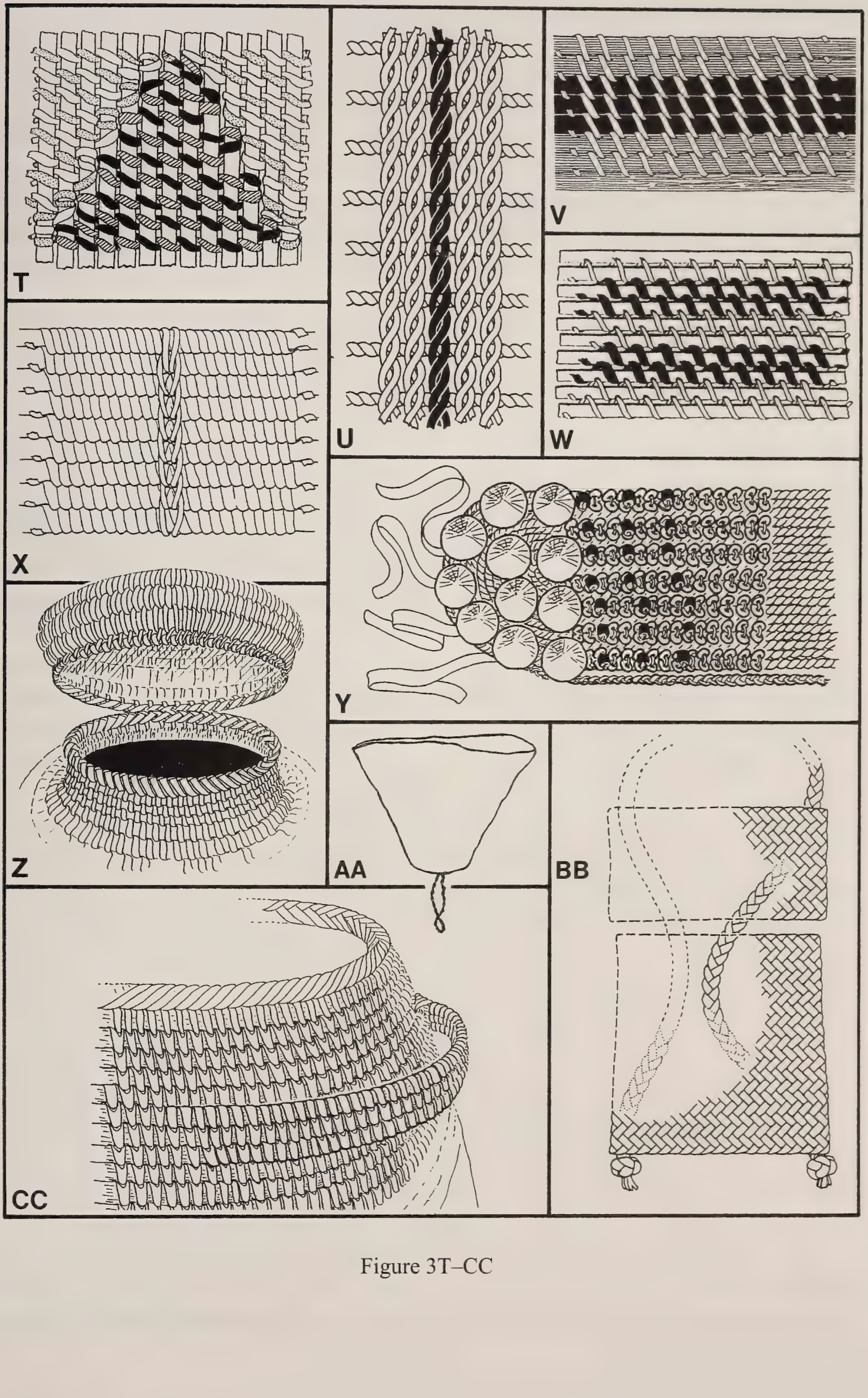


Figure 3T–CC

DESCRIPTION OF BASKETWORK

It has not been possible to identify exactly each basket or item of basketwork for which there is a term in the vocabulary. Some of the terms are dialectical differences for the same object. As many types as are identifiable according to function are recorded. Some objects and shapes seen in old collections, especially baskets with necks, are not identifiable from the contemporary records. Figure 4A–C shows such examples. The records are vague, especially in the use of the term 'Kaffir', but the techniques are recognizable. The fine furcate sewing (Fig. 1Z) was particularly characteristic of the Xhosa and Thembu who settled furthest west.

The following types of object were, and in some cases still are, made.

GARDEN AND GENERAL CARRYING BASKETS

Large garden baskets were used for carrying produce from the fields, for winnowing and for general purposes. Many were being made and used at least up to the late 1980s. The shape was generally an inverted cone, with a flat or concave base, which sometimes had a loop attached to it for hanging. A sketch by Sir Richard England done between 1835 and 1837, however, illustrates a large coiled basket of spherical shape. Baines' sketch (1848) and painting (1873) (Fig. 4D), of a Xhosa woman, also shows a spherical basket.

1. ***itala***: obsolete. Presumed garden basket of Xhosa and Thembu, which most of the early authors do not identify by name. According to Döhne (1844: 41–42), however, *itala* was the largest of the baskets and held two bushels. It was used for carrying produce or to hold grain for immediate use.

Techniques

Not known, but following Döhne (1844: 41) and other early descriptions, and in all antique Xhosa and Thembu baskets seen in museums, they were coiled and sewn with simple (Fig. 1X) or furcate (Fig. 1Z) sewing.

Tools

An awl; an 'iron needle', *isilanda.*

Materials

Sedge (*Cyperus textilis*) (Fig. 5) stems split and de-pithed; the best strands for sewing, and the remainder for the foundation.

Makers

Women.

Records

Early: Hallema 1776 [1932: 132–133], Xhosa. Von Winkelman 1788–1789 [1932:

84–85], Xhosa. Barrow 1797 [1806: 120–121, 157], Xhosa. Alberti 1803–1806 [1810: 62], Xhosa. Bonatz 1834: 352, Thembu, Shiloh. England 1835–1837 [Kennedy 1967: 52, pl. E315], Xhosa or Mfengu. Döhne 1836–1844 [1844: 41–42], Xhosa.

Recent: Nil.

Field survey: Nil.

2. ***umnyazi***: general. A rounded conical basket with slightly concave base that is said to have been common among the Xhosa in the Eastern Cape until recently, and similarly among the Thembu.

Techniques

Fabric: coiled, beeskep sewing over multiple foundation (Fig. 1Y).
Beginning: closed ring (Fig. 1HH).
Method of work: not known.
Shaping: placing of coil (Fig. 2D).
Shape: conical.
Edge: no edging.
Finishing: ends sewn in.
Decoration: none.
Ornamentation: none.

Tools

Not known.

Materials

Foundation: 'grass'; *incaluka* (*Iridaceae*).
Sewing: two-ply cord of twisted sedge.

Makers

Not known.

Records

Early: Nil.
Recent: US Xho. 45, Xhosa. Liverpool 34.129.1, Thembu.
Field survey: Nil.

3. ***ingobozi***: general. Also named *umnyazi*: Xhosa, Bomvana, Mpondo, Xesibe, Bhaca, Vundla; *unyati*: Bhaca. (Fig. 6A–D). This is a soft, flanging basket which was used particularly for carrying produce from the fields. The largest might hold up to 22 kg (Hunter 1936: 85). It was also used for winnowing, when the grain was poured from one basket, held high in the breeze, to another on the ground. It was most often woven in a distinctive split-warp twined weave which is not found elsewhere in southern Africa, except among the Ndzundza of Mpumalanga Province. This is the style of garden basket

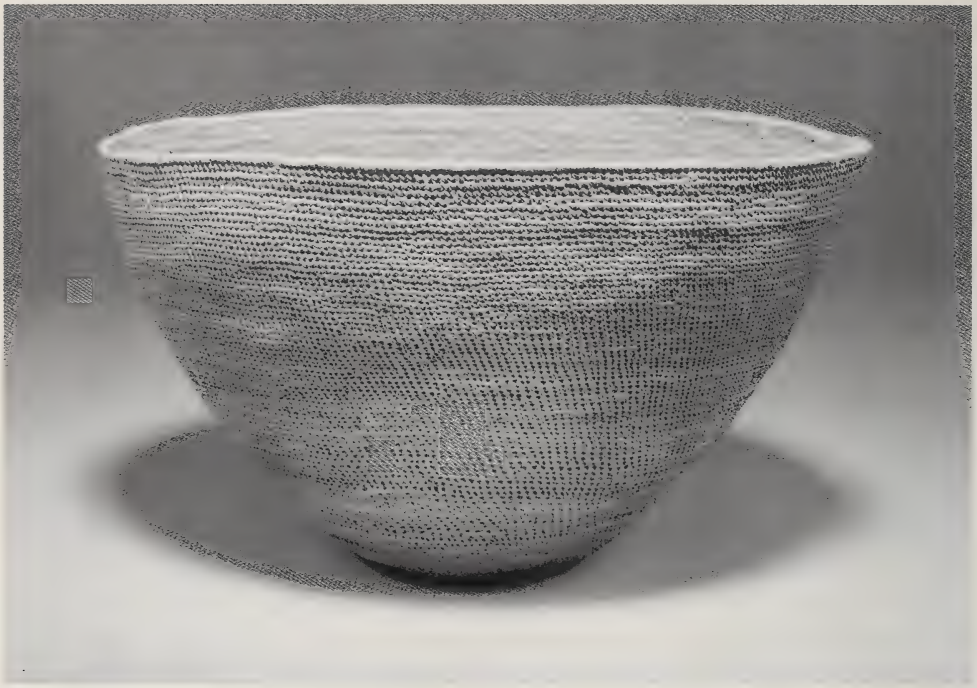


Figure 4A

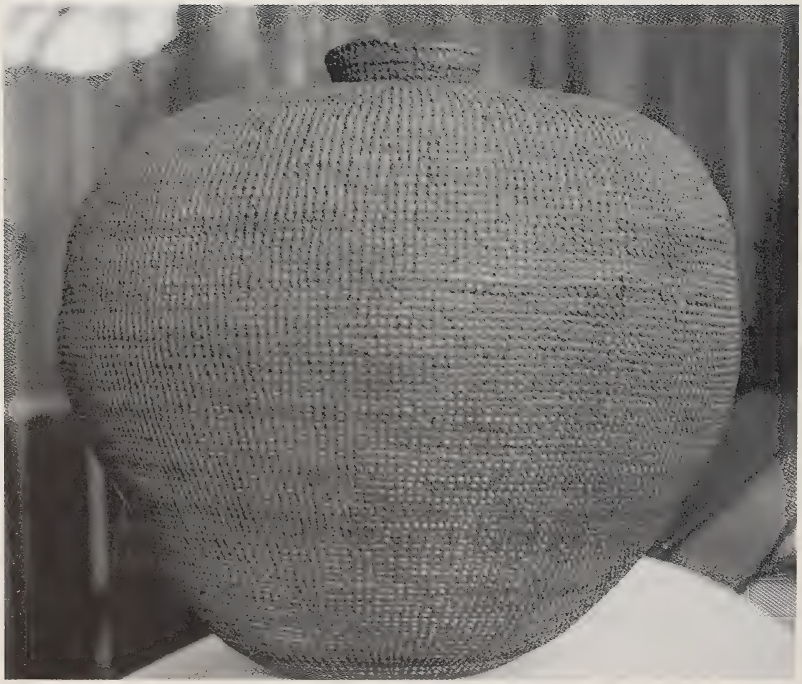


Figure 4B

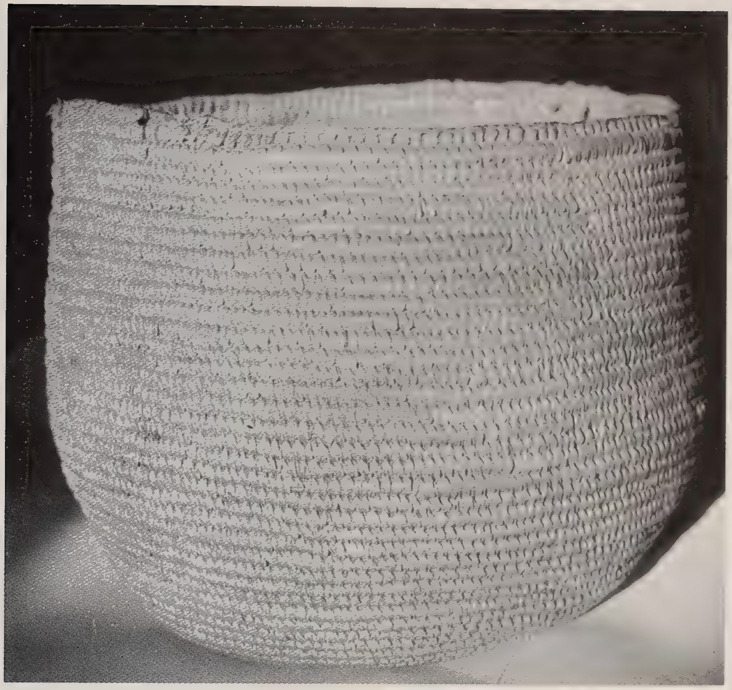


Figure 4C

Figure 4.

Late eighteenth- and nineteenth-century baskets of Xhosa and Thembu.

A. Basket, 'Kaffrer' (Xhosa), near the Sundays River, collected by Sparrman, 1775. Coiled, grass foundation, furcate sewing with split sedge. Height 205 mm. Stockholm 1799.2.101.

B. Narrow-necked basket for holding liquids. 'Kaffir' (Xhosa), purchased *c.* 1891. Grass foundation, corded sedge sewing. Height 275 mm. PR, no number.

C. Basket 'for keeping of milk', Thembu, possibly near Cradock, collected H. M. Naestead, 1852–57. Coiled, furcate sewing with sedge over sedge. Height 164 mm. Copenhagen Gd 52.

D. Basket of maize, Xhosa, Amatola Mountains, painting by Thomas Baines, sketch *c.* 1848, painting 1873. Iziko Museums of Cape Town, Art Collections Division (SANG 1291).

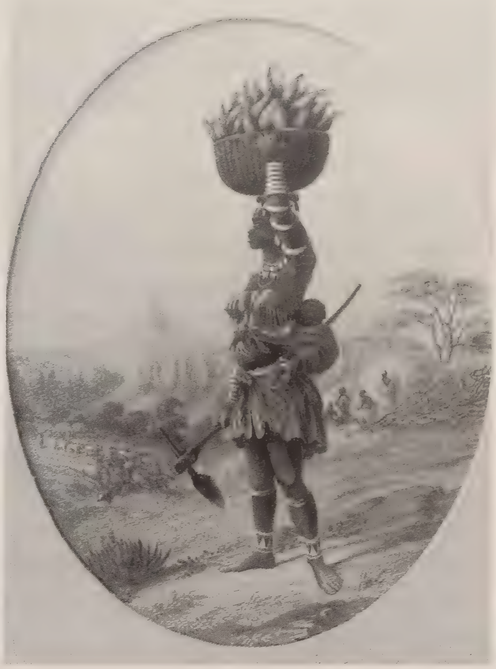


Figure 4D

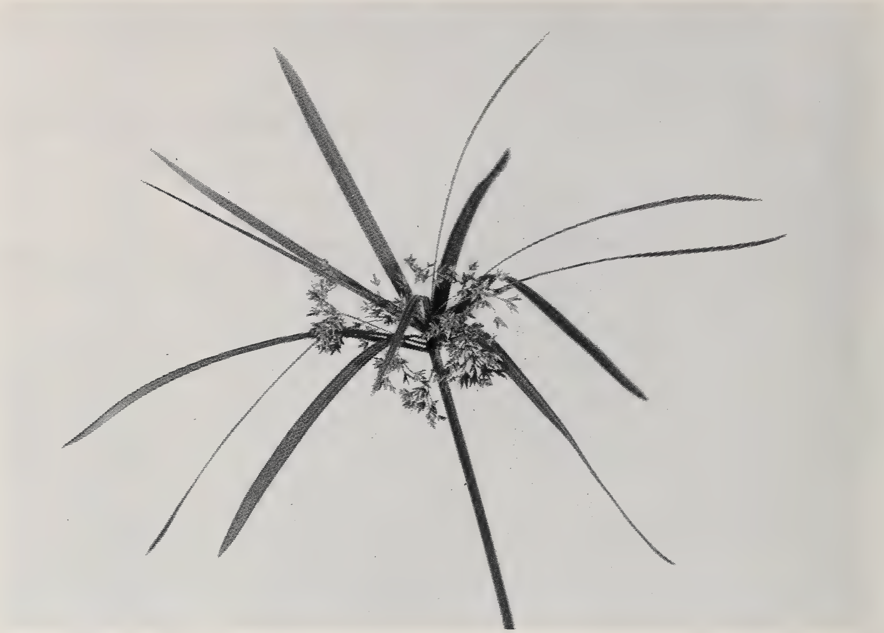


Figure 5

Cyperus textilis.

used most widely in recent times. It was in common use among the Mpondo in the late 1980s. It became known to all groups, but the name *ingobozi* is not mentioned in early accounts of the Xhosa and Thembu, and the basket style and technique are likely to have belonged to later immigrants (Mbo). Those seen among Xhosa and Mfengu in 1971 were made in a variety of plain twine.

Techniques

Fabric: woven, in close split-warp twine, diagonal (Fig. 1M) or zigzag (Fig. 1K) warp; twilled twine (Fig. 1J); plain twine (Fig. 1F); plain or split-warp twine over wide warps.

Beginning: bound warp (Fig. 1DD); looped warp (Fig. 1EE).

Method of work: the material is wetted for use and kept damp while working. Outside faces maker. Moves from right to left (right-handed) (Fig. 6B).

If a conical base is required the work is turned upside down after the base is made and the sides proceed upwards.

Shaping: adding warps (Fig. 2B).

Shape: flanging, with concave base.

Edge: scalloped, with whole warp (Fig. 2L), or with part warp cut (Fig. 2I–K); scalloped, with scalloping warp threaded up to edge and cut (Fig. 2K); last weft sometimes different and stronger; rows of fine twine, or three-ply twine; one row of two-ply bark cord.

Finishing: weft cut off close in fabric.

Decoration: band of different twine, especially plain twine, below edge (Fig. 3G);

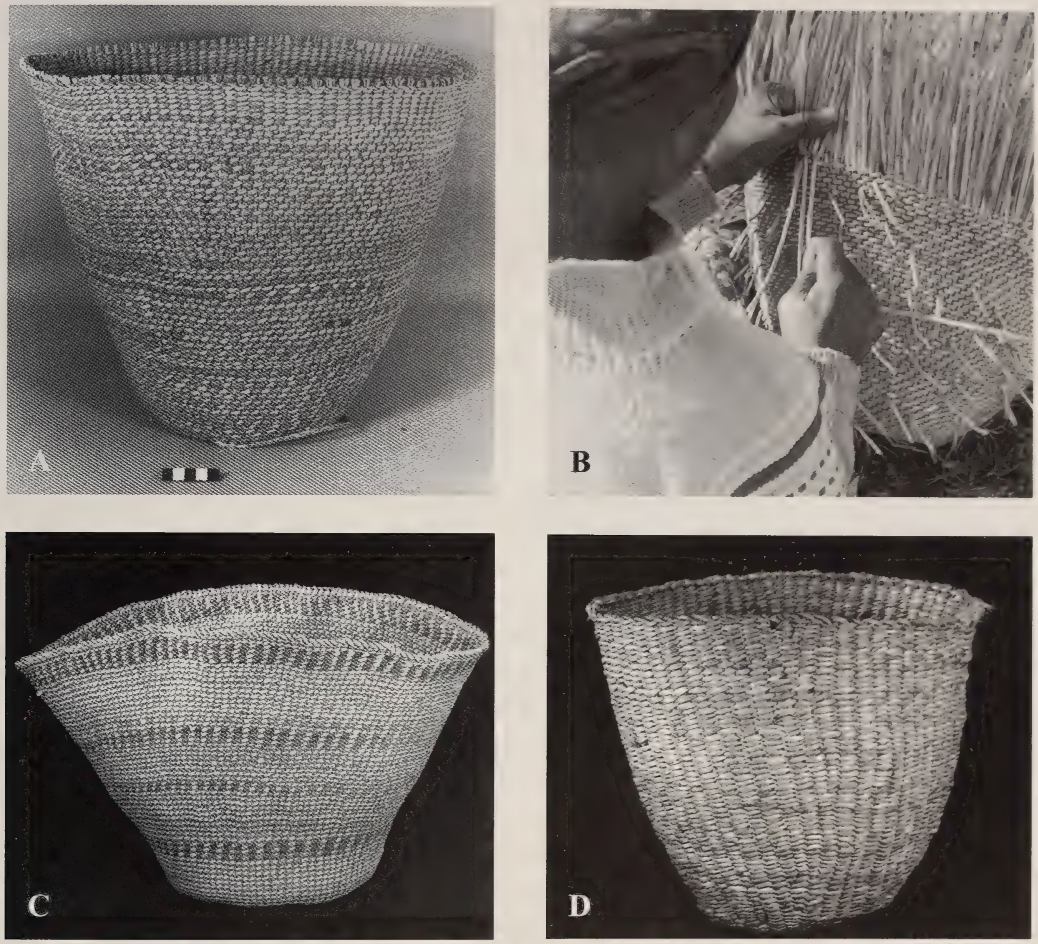


Figure 6

ingobozi, garden basket. A. Mpondo, Libode, D & H, 1984. Height 167 mm. SAM–12728.
B. Mpondo woman making *ingobozi*, Libode, D & H, 1984.
C. Mpondomise, Tsolo, 1938. Height 320 mm. SAM–5973.
D. Xhosa, Kentani, 1969. Height 350 mm. SAM–9601.

band of different coloured material, especially plain or plaited horse hair; bands of same material, different natural colour.

Ornamentation: none.

Utilitarian addition: hanging loop (Fig. 3AA) of two-ply cord or leather.

Tools

Modern knife, formerly a spear blade, for cutting the material.

Materials

Warp: sedge, which grows near the sea or in rivers; grass, especially inland.

Weft: sedge; horse hair (for decoration).

Makers

Women, but not all women are skilled, and some are specialists.

Records

Early: None recognizable.

Recent: Kidd 1904, pls 50, 78, Mpondo. Hunter 1936: 85, 99, Mpondo. Duggan-Cronin 1949: 2, pl. 50, Mpondo. Shaw & Van Warmelo 1974: 162, general. UCT–32/42, 1932, Mpondo, Flagstaff. Liverpool 34.129.2, 1934, Mpondomise. NCHM ET 35/498, 1935, Mpondo, Lusikisiki. SAM–5552, SAM–5622, 1936, Mpondomise, Tsolo. SAM–5973, 1938, Mpondomise, Tsolo. SAM–6058, 1939, Mpondo, Libode. SAM–6009, 1939, Vundla, Port Shepstone. TM 8028, 1939, Xesibe, Mount Ayliff. AM 60.1215, 1960, Mpondo, Port St Johns. EL 5429, EL 5433, 1969, Mpondomise, Tsolo.

Field survey: 1948–1971: Eastern Cape, general. 1969: Xhosa, Kentani, SAM–9601, EL 4791; Mpondo, Libode, SAM–9554, SAM–9563; Mpondomise, Tsolo, SAM–9579. 1984: Mpondo, Libode, SAM–12719, SAM–12727, SAM–12728. 1985: Xhosa, Dwesa, Willowvale, SAM–12763. 1986: Mpondo, Libode, SAM–12871, SAM–12874.

4. ***isiludu***: Thembu, Mpondomise, Bhaca, Hlubi, Mfengu; *isirudu*: Thembu (Engcobo), (Fig. 7A–C); also called *isidladla*, Thembu (Herschel), Mpondomise (Tsolo) (learnt from Hlubi), but *udladla* is a large open-air maize bin.

The Thembu, and some others, who have long had contact with the South Sotho, use a hard, coiled-sewn basket (*cf.* Sotho *seroto*). Where Sotho influence was very strong the sewing strand might be plaited and the base covered on the outside with oxhide, goat- or sheep-skin. The edge might be oversewn with a twist of horse tail hair.

While the use of the term *isiludu* (*isirudu*) indicates that this is a borrowing, nevertheless the Thembu had a long tradition of coiled basketwork.

Techniques

Fabric: coiled sewn, simple or plain beeskep oversewing (Fig. 1X, Y), multiple foundation.

Beginning: knotted foundation (Fig. 1JJ); knotted sewing (Fig. 1KK); open ring foundation (Fig. 1II).

Method of work: several stitches are made before the sewing strand is pulled through and tightened (Hlubi, Sigogo, 1961); outside faces maker, sewn from inside out and right to left (right-handed); sewing material damp.

Shaping: placing of coil (Fig. 2D).

Shape: inverted cone with flat or concave base (Fig. 7).

Edge: no change of stitch but sometimes of material, for example horse hair, which may be plaited.

Finishing: sewing strands cut off close, or knotted separately; coil tapered at edge (Fig. 2CC); base may be covered with ox- or goat-skin.

Decoration: uncommon, two recorded with a single band of different colour; lengthening stitch (Fig. 3Q).

Ornamentation: none recorded.

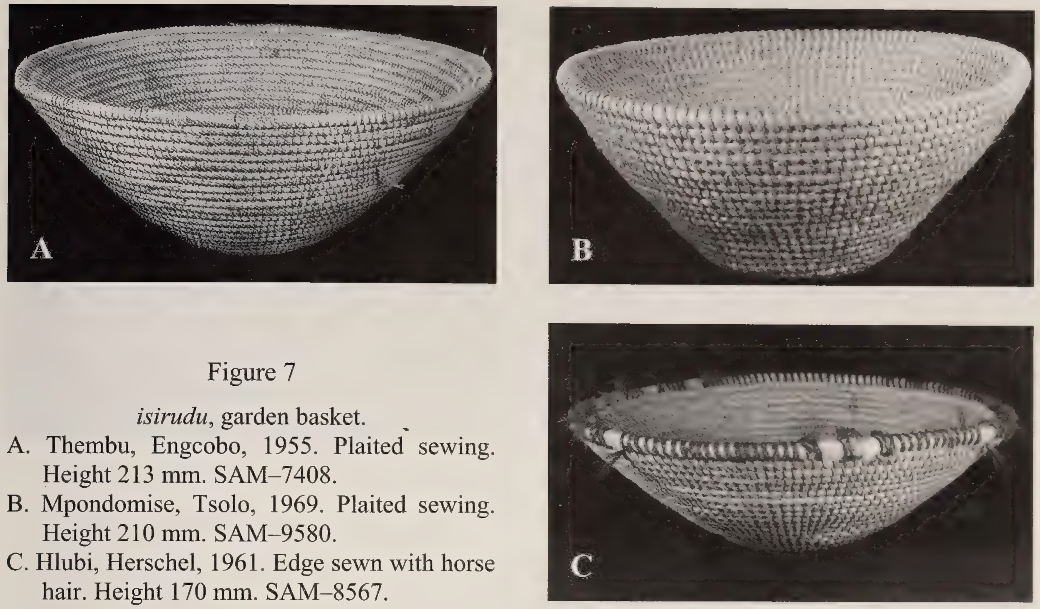


Figure 7

isirudu, garden basket.

A. Thembu, Engcobo, 1955. Plaited sewing. Height 213 mm. SAM–7408.
B. Mpondomise, Tsolo, 1969. Plaited sewing. Height 210 mm. SAM–9580.
C. Hlubi, Herschel, 1961. Edge sewn with horse hair. Height 170 mm. SAM–8567.

Tools

Modern knife; awl; two modern steel needles, one flat the other curved (Hlubi, Matatiele, 1961); sailmaker's needle.

Materials

Foundation: grass.

Sewing: grass, plaited or often two-ply twisted grass, agave fibre, sedge, or *Iridaceae* leaf.

Decoration: Horse tail hair or dyed material.

Makers

Mainly men, but women too.

Records

Early: Nil.

Recent: Cornner (correspondence) 1936, Mpondomise, Tsolo. Shaw & Van Warmelo 1981: 233, 238, 404, 409, general. NCHM ET 35/465, 1935, Thembu, Xalanga. EL 5499, 1969, Thembu, Qebe Valley.

Field survey: 1955: Thembu, Engcobo, SAM–7408. 1961: Hlubi, Matatiele; Hlubi, Herschel, SAM–8543, SAM–8567. 1969: Thembu, Engcobo; Mpondomise, Tsolo, SAM–9580.

GENERAL PURPOSE BASKETS

Smaller baskets of different sizes were used for general carrying or holding purposes. These baskets were of the same techniques and materials as the garden baskets, that is, those formerly made by the Xhosa and Thembu were sewn and those of the others woven. The dominant material for both sorts was sedge, but grass was greatly used for coil foundation or warp.

1. ***inzwazwa***: obsolete, Xhosa; *umzwazwa*: large basket (one bucket), Xhosa (Döhne 1844); *ingceke* (Fig. 8A): Xhosa, Mpondo, Mpondomise, Xesibe, Nzimakwe; *ingcebe*: Xesibe; *ijomo*: Xhosa, obsolete; *umnyazi*: general (Fig. 8B, C), except Hlubi and Mfengu.

Technique

The same as for *ingobozi.*

Records

Early: Döhne 1836–1844 [1844: 41–42], Xhosa.

Recent: Müller 1926: 23, 42, Hlubi. Shaw & Van Warmelo 1981: 409–410, general.

Field survey: 1948: Mpondo, Lusikisiki, SAM–6684. 1955: Mpondo, Bizana, SAM–7386. 1961: Vundla, Quthing, SAM–8541. 1969: Mpondomise, Tsolo, SAM–9577; Bhaca, Mount Frere.

2. **No name**. A tiny roughly-made coiled basket (height 60 mm) with a handle (Fig. 9). It is used for holding white beads and other precious things when they are put into the river as a ritual offering.

Techniques

Fabric: furcate sewing, twice into one hole, on multiple foundation (Fig. 1Z).

Beginning: open ring.

Shape: small, bowl-shaped, with handle.

Edge: no edging.

Tools

Not known.

Materials

Split palm-leaf sewing over palm-leaf midrib foundation.

Makers

Not known.

Records

Early: Nil.

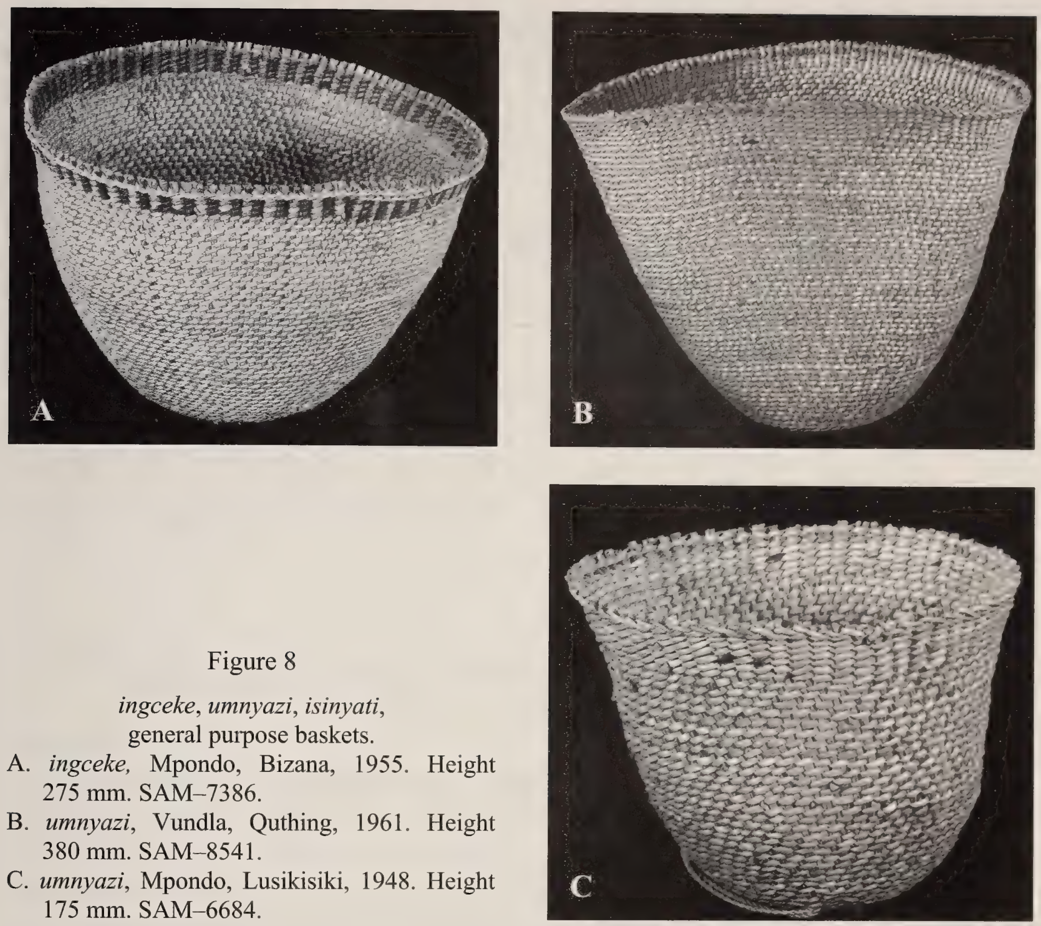


Figure 8

ingceke, *umnyazi*, *isinyati*,
general purpose baskets.

- A. *ingceke,* Mpondo, Bizana, 1955. Height 275 mm. SAM–7386.
- B. *umnyazi*, Vundla, Quthing, 1961. Height 380 mm. SAM–8541.
- C. *umnyazi*, Mpondo, Lusikisiki, 1948. Height 175 mm. SAM–6684.

Recent: Albany Museum, no number. Hammond-Tooke 1975: 21.

Field survey: Nil.

3. **Modern baskets**. During the last two centuries, other styles, both of shape and technique, and the addition of lids and handles, have been introduced, largely through the schools (Fig. 10). They have not all been suited to the older purposes. The Mfengu in the Peddie district, who were more exposed or more susceptible to foreign influences in the early 19th century, made coiled sewn baskets of split palm-leaf or sedge, with lids and handles. A Thembu *isiludu* was seen with openwork sewing, an introduced technique. The Mpondo near Port St Johns learnt how to make an entirely different style of basket, of German origin, primarily for sale, but they are used by the makers as well (Fig. 11).

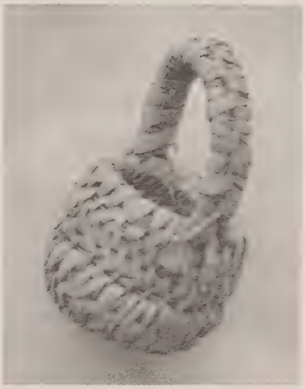


Figure 9

Basket for ritual offering, Xhosa, Eastern Cape, *c.* 1969.
Height 60 mm
Albany Museum, no number.

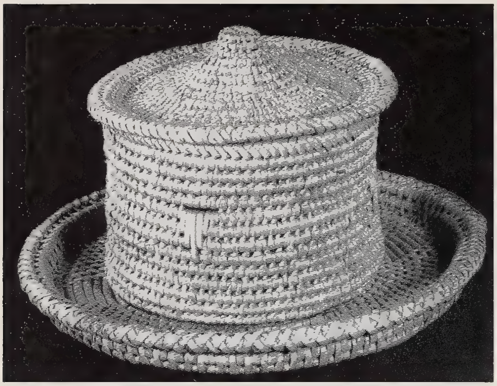


Figure 10

Basket and tray, schoolwork, probably Mpondomise, St Cuthbert's Mission, Tsolo, 1937. Height of basket 178 mm. SAM–5852.

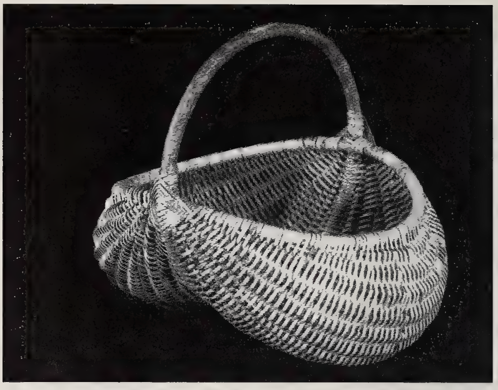


Figure 11

Port St Johns basket, German origin, Mpondo, Port St Johns, 1961. Height including handle 248 mm. SAM–8456.

Records

Early: Nil.

Recent: 1937, Mpondomise, Tsolo, SAM–5852. Eastern Cape, SAM–7141.

Field survey: 1968: Mpondo, Port St Johns, SAM–8456.

VESSELS FOR FOOD AND LIQUIDS

MILK VESSELS

The most famous baskets of former times, mentioned frequently in the literature, were those used for holding milk, and in the west as milk pails. Döhne (1844) gave their size as about half a bucket, but this must have been an average as larger ones have been seen. According to Morgan (1833: 48) and Kropf (1889: 101), the small ones were used to drink out of. Such baskets are recorded in the literature up to 1901, and according to Bhaca testimony were used by some up to 1948, but they gave way to the easy availability of new containers, because it was no longer worth the effort of making them, and they are now obsolete. A few survive in museums. They were made of sedge, in the coiled sewn technique, generally with the very fine furcate sewing not seen nowadays in this area nor elsewhere in southern Africa. De Mist (1835: 114) stated that they were smeared with fat before use, but their watertightness depended, as did that of the Khoisan roofing mats, on the swelling of the materials when damp. In Stockholm, Copenhagen and Oxford, the surviving examples are of Xhosa and Thembu origin. The technique was still to be observed in 1948, and rather rough examples were seen then among the Bomvana (whom Carter (1927: 60) may have meant by the name 'Mambookie' among whom he saw such milk baskets in 1782). For actual milking, Bomvana, Mpondo, Xesibe and Bhaca used wooden pails. According to estimates, the size of the baskets varied from one to eighteen litres capacity.

1. ***ithunga***: obsolete, Xhosa and Thembu. Basketwork milk pail, for milking into or for holding milk (Figs 12, 13); still known and used for holding milk by Hlubi up to 1901, and some Bhaca in 1948. *Ithunga* now generally means a milk pail of any material. *Imbenga*: obsolete, Xhosa and Thembu, a milk vessel.

Techniques

Fabric: coiled sewn with fine furcate sewing on multiple foundation (Fig. 1Z).
Beginning: closed ring of foundation (Fig. 1HH); knot in sewing (Fig. 1KK).
Method of work: not known.
Shaping: placing of coil (Fig. 2D).
Shape: bowl-shaped, some with walls slightly incurved to mouth.
Edge: plain oversewing; oversewing two-ply cord; blanket-stitch (Fig. 2BB).
Finishing: not known.
Decoration: spaced vertical lines of sewing (Fig. 3Q).
Ornamentation: none.
Utilitarian addition: handle (Fig. 3CC); lid (Fig. 3Z).

Tools

No reference, but an awl must have been used.

Materials

Foundation: stripped sedge; grass.
Sewing: stripped sedge, plain or twisted.
Decoration: two-ply cord of plant fibre.

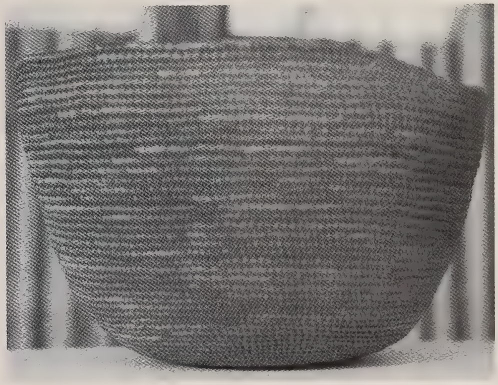


Figure 12

ithunga, an obsolete basket for holding milk or in this case 'for holding water', travelling 'Kaffir' (Emigrant Xhosa). Collected by Burchell, 1811, Kanna Kraal, between Fraserburg and Carnarvon. Height 160 mm.
PR 1886.1.468 (Ashmolean Collection).

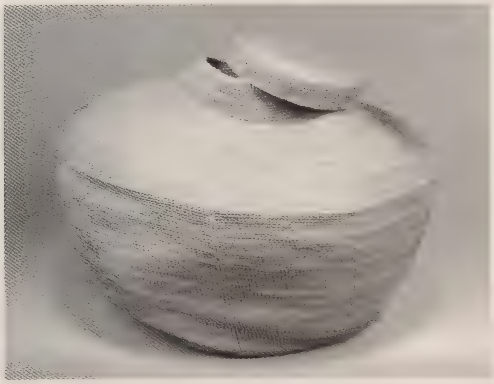


Figure 13

?*ithunga*, milk storage basket, mid-1790s. Fine furcate sewing. Height 285 mm.
Stockholm 187.1.258 (Afzelius Collection).

Makers

Women.

Records

Early: (A few records have been selected out of the very many references to these baskets.) Sparrman 1775 [1785: 34–35, pl. 1], Gonaqua. Stockholm 1799.2.101, Gonaqua or Xhosa, collected by Sparrman, 1775. Hallema 1776 [1932: 132], Xhosa. Gordon 1777 [1988: 106], Xhosa, Great Fish River. Carter 1782 [1927: 60–61], Mbo. Le Vaillant 1782 [1797: 364], Gonaqua. Von Winkelman 1788–1789 [1932: 85], Xhosa. Barrow 1797 [1806: 120–121, 157], Gonaqua. Stockholm 187.1.258, mid-1790s. Stockholm RES 1623, 1799, Gonaqua. De Mist 1803 [1835: 114], Xhosa. Lichtenstein 1803–1806 [1811: 449, 665], Xhosa. Alberti 1803–1806 [1810: 37], Xhosa. Burchell 1811 [1953: 190]. PR 1886.1.468, 1811, Emigrant Xhosa, near Fraserburg, collected by Burchell. Hallbeck & Fritsch 1827 [1826: 307], Thembu. Kay 1827 [1833: 123, 126], Xhosa. Morgan 1833: 48, Xhosa. Bonatz 1834: 350, 352, Thembu, Shiloh. Döhne 1836–1844 [1844: 41–42], Xhosa. Backhouse 1839 [1844: 183, 225, 252], Xhosa, Kei River. King 1851–1852 [1853: 164], Mfengu. Copenhagen Gd 52, 1857, Thembu. Walker 1851 (*in* Backhouse & Tylor 1862): 360, Xhosa. Nauhaus 1881: 343–344, Xhosa. Kropf 1846–1889 [1889: 100], Xhosa.

Recent: Scully 1901: 45, Hlubi. Schönland 1905: 131, ?Xhosa, ?Mfengu, Grahamstown. Müller 1926: 23, 42, Hlubi. Duggan-Cronin 1939: 28, Xhosa. Tyrrell 1968: 168, Mpondo. Shaw & Van Warmelo 1981: 260, 264, 410, 411, general.

Field survey: 1948: Eastern Cape, none seen.

VESSELS FOR FOOD AND DRINK

Other baskets of various sizes, for serving food or for drinking or holding beer or water, and either bowl- or beaker-shaped, were called *isitya,* irrespective of which shape or purpose. Those of Xhosa (Döhne 1844: 42) and Thembu, now no longer seen, appear to have been of the same technique and materials as the milk baskets above. In the east, palm-leaf is used for the sewing of such baskets, coiled sewn with simple oversewing, on either a grass or a palm-leaf foundation, and sometimes decorated with diaper patterns. The beaker-shaped beer baskets, though not as well documented as the milk baskets, are almost as renowned.

2. ***isitya***: obsolete, Xhosa (Lichtenstein 1811, *sihtja*) for milk or food; Mpondo, Xesibe for food or beer; Bhaca said to be for food only, but some beer baskets so named were seen at Mount Frere in 1969. (Fig. 14A–D)

3. ***iqaku***: Xhosa, a small cup; Mpondo, for drinking, especially for infants; not generally known.

4. ***umnyazi***: Mpondo, Mpondomise, a measure for dry foods; Xhosa, Bomvana, Mpondomise, Xesibe, Vundla, a smallish basket.

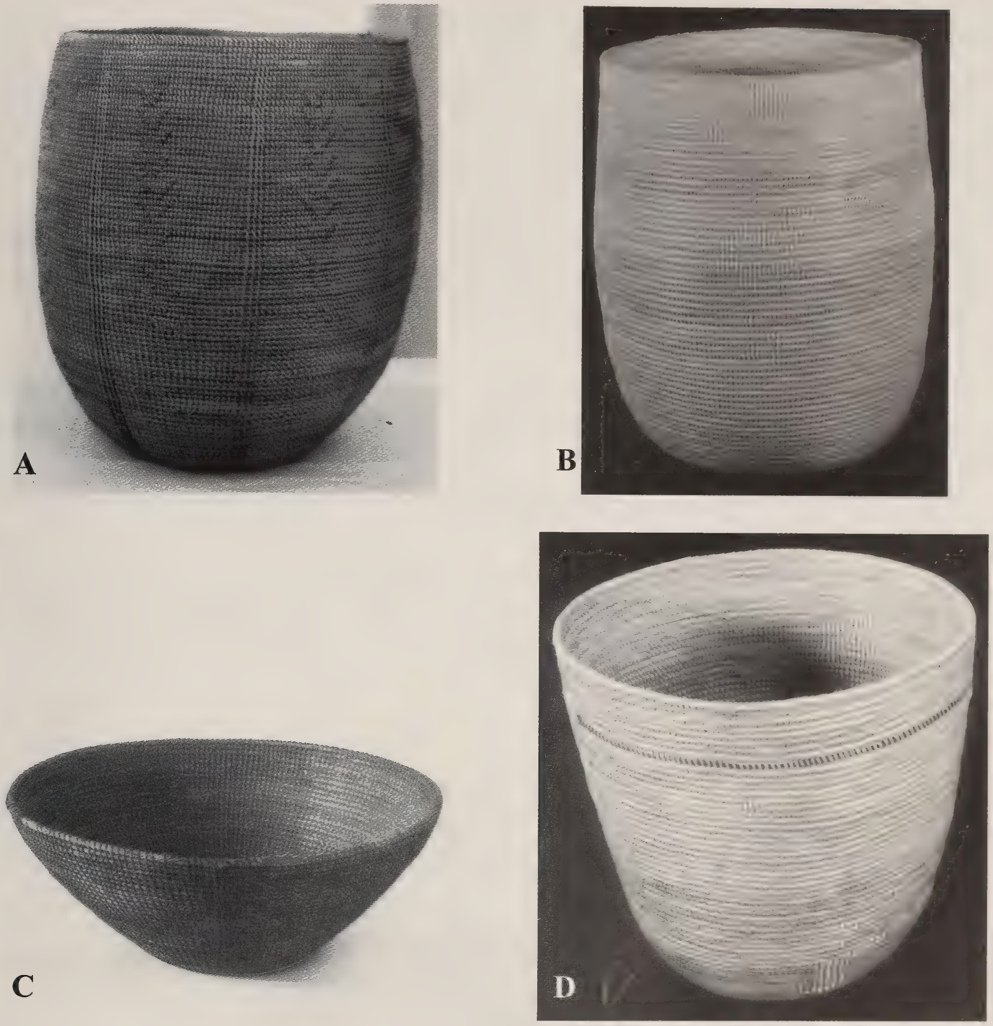


Figure 14

isitya, beer beaker (A–C) or food basket (D).
A. Mpondo, Flagstaff, 1932. Height 256 mm. UCT–32/41.
B. Mpondo, Umvume Springs, 1939. Height 294 mm. SAM–5994.
C. Mpondo, Libode, 1942. Width 222 mm. FH 369. Photo N. J. van Warmelo.
D. Xesibe, Mount Ayliff, 1969. Height 225 mm. SAM–9633.

5. ***ingcaza***: Bhaca, for drinking beer.

6. ***ingceke***: Vundla, a small basket for food; Xhosa, Mpondo, Xesibe, a small *ingobozi*.

7. ***ilala***: made of palm-leaf, for food or drink; this would mean a coiled sewn basket like *isitya* above.

Techniques

isitya, iqaku

Fabric: Xhosa, Thembu: obsolete, close furcate or simple sewing over multiple foundation (Fig. 1X, 1Z). Mpondo, Xesibe, Bhaca: coiled, simple oversewing, over multiple foundation (Fig. 1X). Xesibe: widely spaced sewing. Bhaca (Ixopo): woven, split-warp twine.

Beginning: chequer square (Fig. 1LL); closed ring (Fig. 1HH) (including Xhosa obsolete); open ring (Fig. 1II); bent foundation (Fig. 1GG).

Method of work: not known.

Shaping: placing of coil (Fig. 2D).

Shape: for food, shallow, widely flanging, sometimes with rounded base; for beer, straight-sided or slightly narrowed at mouth, usually on a flat base (Fig. 14). Bhaca (Ixopo) only slightly flanging sides.

Edge: herring-bone (Fig. 2DD) or close diagonal oversewing (Fig. 2EE) or close plain oversewing (Xhosa, obsolete).

Finishing: ends tucked inside, under two stitches below.

Decoration: diaper pattern by lengthening stitch (Fig. 3Q), by making raised pattern or half-hitching sewing strand round neighbouring stitch (Fig. 3R).

Ornamentation: none.

umnyazi: See *ingobozi.*

Tools

Xhosa and Thembu, presumed awl; Mpondo, awl.

Materials

Foundation: sedge, Xhosa, Thembu and Bhaca; grass or palm-leaf strips, Mpondo, Xesibe.

Sewing: palm-leaf, Bhaca.

Makers

Xhosa and Thembu women; Mpondo and Xesibe men.

Records

Early: Lichtenstein 1803–1806 [1811: 655], Xhosa. Döhne 1836–1844 [1844: 42], Xhosa. Baines 1849 [1961: 138], Xhosa. Stanford 1889 [1958: 124], Mpondo.

Recent: MM 1830, 1913, Bomvana or Mpondo. Müller 1926: 42, Hlubi. Hunter 1936: 99, 359, Mpondo. Duggan-Cronin 1949, pl. 53, Mpondo. Shaw & Van Warmelo 1981: 405, 410, 411, 413, general. UCT–32/41, 1932, Mpondo, Flagstaff. NCHM ET 35/454, 1935, Bomvana. SAM–5994, 1939, Mpondo, Umvume Springs. SAM–6068, 1939, Mpondo, Libode. FH 369, no date, Mpondo. SAM–10505, SAM–10506, 1974, Port St Johns, Mpondo.

Field survey: 1969: Mpondo, Libode; Xesibe, Mount Ayliff, SAM–9633.

STORAGE BASKETS

Baskets were, but are seldom any longer, used for the storage of clothing, ornaments, household goods and small articles.

Narrow-necked, lidded, globular baskets (Fig. 4), possibly for storage of liquids or left-overs, have been seen in museum collections, where they were attributed to this area, but not all the attributions have been confirmed. All are coiled sewn, two of palm-leaf, with simple sewing, one of grass with furcate sewing, and one of sedge with simple oversewing (Copenhagen Gc 420, 1873, Cradock; Cambridge, 1882.42, Cape Colony, 'Kafir', 'for storing milk').

FOR CLOTHING, ORNAMENT AND HOUSEHOLD GOODS

1. ***iqindiva***: Xhosa, obsolete. Used for clothing, household goods and small things. Döhne (1844: 41–42) stated that it held two buckets, and Nauhaus (1881: 344) described it as a large trunk, about 90 by 50 cm. There is no indication of shape, but see Figure 15, an oval basket, described as a woman's basket (PR 1884.44.12, Thembu, 1827).

2. ***itala***: Xhosa, large basket.

Techniques

Fabric: these are coiled sewn baskets (Fig. 1X–Z).
Beginning: (*iqindiva)* bound oval (Fig. 1GG).
Edge: (*iqindiva*) herring-bone (Fig. 2DD).

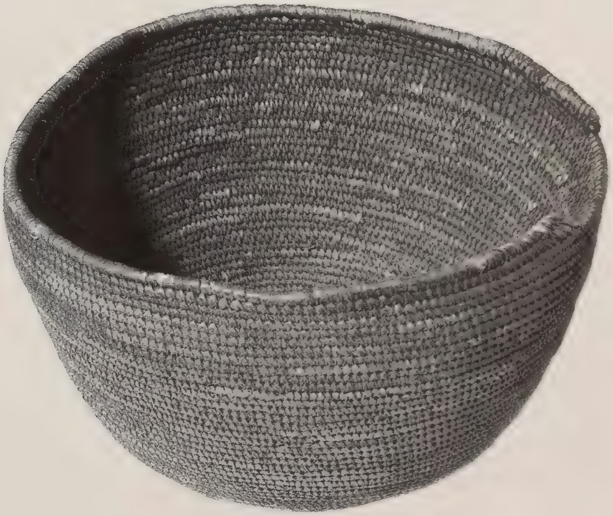


Figure 15

iqindiva, for storing clothes or small household things, Thembu, 1827. Height 300 mm. PR 1884.44.12.

Material

Palm-leaf.

Records

Early: Döhne 1836–1844 [1844: 41–42], Xhosa. Nauhaus 1881: 343, Xhosa. Kropf 1846–1889 [1889: 101], Xhosa. PR 1884.44.12, Thembu, 1827.

Recent: Cambridge 58.1.1901.

Field survey: Nil.

FOR SNUFF

Nauhaus (1881: 343) claimed to have seen a small basketwork snuff-box, shaped like a gourd, with a tight lid. There is no confirmation of this.

Techniques (according to Nauhaus 1881)

Fabric: coiled sewn.
Beginning: not known.
Shaping: placing of coil (Fig. 2D).
Shape: gourd-shaped.
Edge: not known.
Finishing: not known.
Decoration: not known.
Ornamentation: none.
Utilitarian additions: lid, handle.

Tools

Not known.

Materials

Foundation: grass.
Sewing: 'bast'.

Makers

Not known.

Records

Early: Nauhaus 1881: 343, Xhosa.
Recent: Nil.
Field survey: Nil.

BAGS

GENERAL

The following loosely woven bags were used:

1. ***umngqungu***: Xhosa, Bomvana, Mpondo, for holding tobacco; Bomvana, for collecting fish. *ixamba*: Mpondo, for holding tobacco for sale in one piece; for holding sprouted maize (Van Warmelo pers. comm. 1958) (Fig. 16); Mpondo, Libode, for holding dry tobacco (Davison & Hooper pers. comm. 1985).

2. ***umgodlo***: a bag made of *ikhwane* rushes, Thembu and others (cf. South Sotho *mokotlo*) (Shaw & Van Warmelo 1981: 232).

3. ***uzwazwa***: Bomvana, Mpondo, for carrying fish (Fig. 17).

Techniques

Fabric: open plain twine (Fig. 1G); open (Fig. 1L) or close (Fig. 1K) split-warp zigzag twine.

Beginning: warps laid side by side and joined by first row of twined weft, then bent at centre (Fig. 1AA).

Method of work: not known.

Shaping: tension.

Shape: umngqungu, long oval with handle; *uzwazwa*, rectangular.

Edge: four rows of close twine in same or opposite direction (Fig. 2O, P).

Finishing: ends cut off.

Decoration: none.

Ornamentation: none.

Utilitarian addition: handle.

Tools

If any, not known.

Materials

Warp: for tobacco bag, thick sedge (*ikhwane*), *Cyperus latifolius* Poir.; for fish bag, a thinner sedge.

Weft: grass or sedge.

Handle: sedge.

Makers

Women.

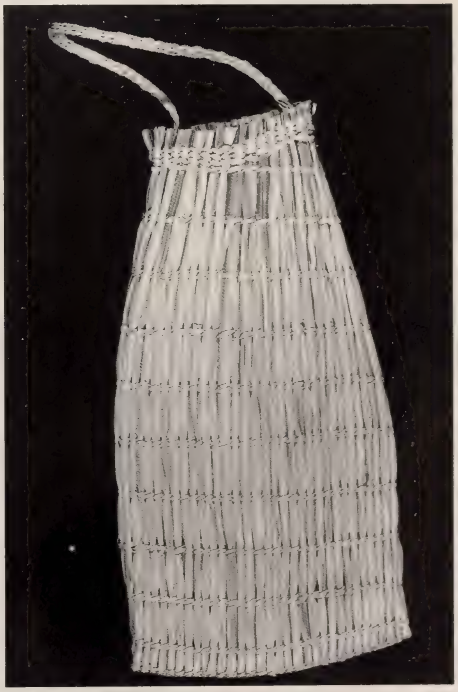


Figure 16

umngqungu, *ixamba*, tobacco bag, Mpondo, Libode, 1939. Length 445 mm. SAM–6059.

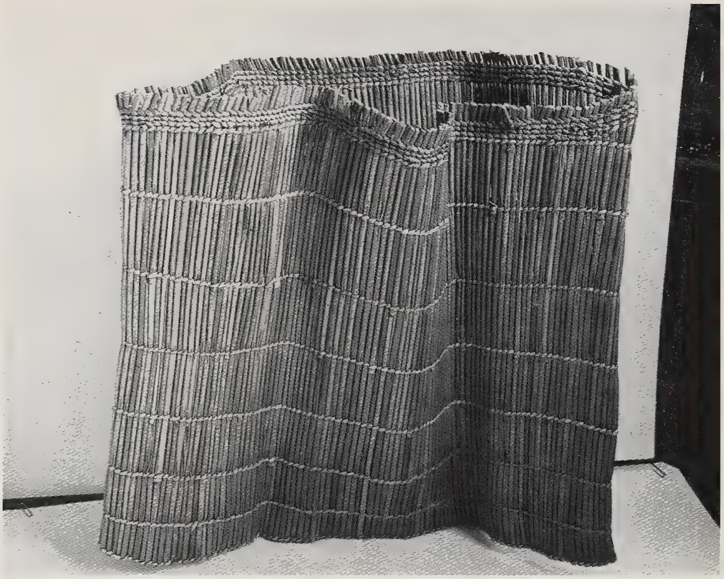


Figure 17

uzwazwa, fish or shrimping bag, Mpondo, Libode, 1939. Height 470 mm. SAM–6057.

Records

Early: Nil.

Recent: Cambridge 34.107, 1934, Ngqeleni, Mpondo. NCHM ET 35/450, NCHM ET 35/467, 1935, Elliotdale, Bomvana. SAM–6057, SAM–6059, 1939, Umvume Springs, Mpondo. Shaw & Van Warmelo 1981: 232, 374–375, Xhosa, Bomvana, Mpondo.

Field survey: 1969: Mpondo, Libode. 1985: Mpondo, Libode (D & H).

FOR SEEDS

4. ***intlwayelelo***: Bomvana, otherwise not known. A small oval basket with a narrow neck and a strap by which it was held (Fig. 18). Used for holding the seeds while sowing.

Techniques

Fabric: close or open diagonal, or open zigzag, split-warp twine (Fig. 1K, L, M).

Beginning: bound warp (Fig. 1DD).

Method of work: not known.

Shaping: pairing or adding warps (Fig. 2A, B).

Shape: ovoid.

Edge: half warp bent forward to right into last row of twine.

Finishing: not known.

Decoration: band of close diagonal split-warp twine at neck on body of open zigzag split-warp twine.

Ornamentation: none.

Utilitarian addition: a cord or three-strand simple plait.

Tools

Not known.

Materials

Warp and weft: sedge.

Makers

Not known, but likely to have been women.

Records

Early: Nil.

Recent: NCHM ET 35/354, NCHM ET 35/355, NCHM ET 35/364, 1935, Elliotdale, Bomvana. Shaw & Van Warmelo 1981: 232, 239, Bomvana.

Field survey: 1948: Bomvana, Elliotdale.

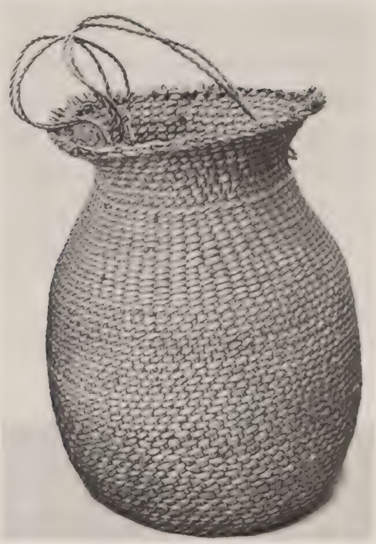


Figure 18

intlwayelelo, basket for holding seed while sowing, Bomvana, Elliotdale, 1935. Height *c.* 200 mm. NCHM ET 35/354.

POUCHES

5. ***isikwamu***: Nzimakwe. In the eastern area of the Eastern Cape, a twilled pouch, such as is characteristic of the east coast of Africa, is sometimes used. It is seen among the Mpondo, Xesibe and Nzimakwe, and an isolated example (SAM–4938), came from the Lesotho border. It consists of two parts, one of which is slightly larger than the other and fits over it as a lid which slides up and down on the plaited palm-leaf cord handle that passes inside both parts. It is used for carrying small quantities of food, or, more particularly, by doctors for carrying medicine. It is possible that examples are bought from KwaZulu-Natal, and not made locally (Fig. 19).

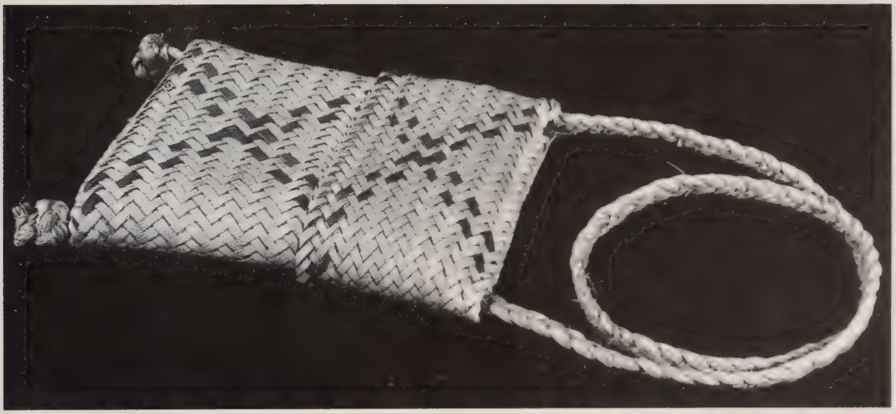


Figure 19

isikwamu, pouch, Nzimakwe, Port Shepstone, 1939. Height 200 mm. SAM–6005.

Techniques

Fabric: woven, diagonal twill over two (Fig. 1B).

Beginning: elements knotted in pairs (Fig. 1BB).

Method of work: each part is woven separately as a cylinder, one to fit over the other.

Shaping: each cylinder pressed flat and one end sewn to close it.

Shape: rectangular.

Edge: elements back on tracks making a double edge (Fig. 2F).

Finishing: knots turned in and edges of the bend sewn together invisibly to close the base (Fig. 3F).

Decoration: a cross on back and front by using the same material dyed (Fig. 3S).

Ornamentation: none.

Utilitarian handle: plaited palm-leaf, knotted outside, runs inside (Fig. 3BB).

Tools

A sharp tool for sewing the base.

Materials

Fabric and handle: *Hyphaene coriacea*, leaf folioles split.

Dyes: *mtsekisane* (*Euclea* sp.) and *isimoyo (Acacia* sp.)

Makers

Not known.

Records

Early: Nil.

Recent: SAM–6005, 1939, Nzimakwe, Port Shepstone.

Field survey: 1955: Mpondo, Bizana. 1969: Xesibe, Mount Ayliff.

GRAIN BINS

A basket bin for bulk storage of grain is not a Southern Nguni feature. Their custom was to store the grain harvest in pits, preferably under the cattle enclosures. In the north of the area, however, along the Lesotho border, where Thembu, Bhaca and some Xhosa have long been in contact with South Sotho and later with Hlubi, the habit of storing grain in large baskets was adopted by a few (Fig. 20). Where the Zulu word *isilulu* is used for the bin, it may be that the custom was adopted from Mfengu or Hlubi rather than from Sotho. Latterly, the bins have mostly been replaced by grain bags or disused oil drums.

1. ***isilulu***: Xhosa, Herschel; Thembu, Engcobo; Bhaca and Hlubi, Mount Frere (Fig. 20A); Hlubi, Herschel; *isiximba*: Bhaca, Mount Frere. A large, ovoid basket that varies in size from about 60 to 150 cm high, and which holds from 5 to 30 bags of grain. It is kept on a platform of stone, indoors (Bhaca) or outdoors (Hlubi), and used for the storage of grain. If outdoors, it is sometimes plastered on the outside with a mixture of cowdung and mud.

The opening at the top is closed with a flat stone (Hlubi), or a small mat (Bhaca). The Hlubi hold the bin upright by attaching it by ropes to a tripod of saplings placed over it. The bins are made each year about July, their numbers in accordance with the expected size of the harvest. According to Bhaca, an *isiximba* is built on to a sledge and plastered. There is a drawing by C. Bell 'A Caffre Basket' (Fig. 20B) that has a similar shape, but 'Caffre' usually denotes Xhosa or Thembu.

Technique

Fabric: coiled, with multiple foundation about 2 cm thick, very loose simple, or widely spaced beeskep oversewing (Fig. 1Y); sewing strand sometimes plaited.

Beginning: not known.

Method of work: not known.

Shaping: placing of coil (Fig. 2D).

Shape: ovoid, narrowing to small mouth.

Edge: oversewn with grain-bag twine.

Finishing: not known.

Decoration: none.

Ornamentation: none.

Tools

Modern, for sewing, a needle made from a bucket handle, Hlubi.

Materials

Foundation and sewing: coarse thatching grass, *Hyparrhenia* sp.; sewing sometimes a three-strand simple plait of grass.

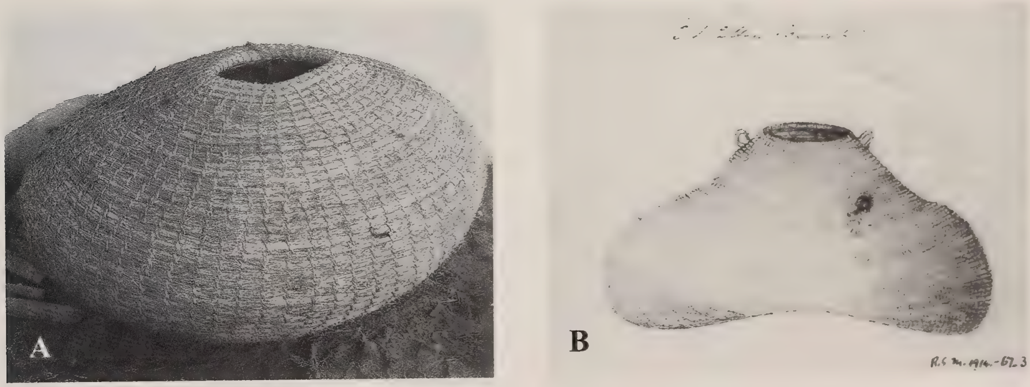


Figure 20

isilulu, *isiximba*, grain bin.

A. Bhaca or Hlubi, Lugangeni, Mount Frere, 1948. Photo N. J. van Warmelo.

B. 'Caffre' basket which has the appearance of a grain bin. Drawing by C. Bell, *c.* 1836. Photo Cape Archives.

Makers

Men.

Records

Early: Perestrello 1554 [1898: 236], ?Mpondo, near Msikaba River. Bell 1836, drawing, ?Xhosa. Weitz 1876: 327, Hlubi.

Recent: Müller 1926: 42, Hlubi. Department of Agriculture and Forestry 1940, Xhosa. Shaw & Van Warmelo 1972: 97, Hlubi.

Field survey: 1948: Bhaca, Mount Frere. 1961: Hlubi, Thembu, some Xhosa, Herschel. 1969: Thembu, Engcobo; Mpondomise, Tsolo.

FOOD MATS

Small mats were made in a variety of shapes, circular, semi-circular or half oval, but most commonly quadrilateral. Among the Mpondo the edges of the circular mats are sometimes turned up to form a shallow bowl. The larger examples are used to catch the meal as it falls from the grinding stone; an example was seen in Mpondoland large enough to serve four stones at once, but commonly each stone has its mat. The smaller examples are used as dishes for food. They form the symbol for relationship groups in small communities (Hammond-Tooke 1963), and are often given as gifts. Recently they have been sold in shops.

1. ***isithebe***: general (Fig. 21A–E).

Techniques

Fabric: plain close twine (Fig. 1E); chain stitch twine (Fig. 1I).

Beginnings: for quadrilateral shape, warps laid flat and joined by twining (Fig. 1AA); for circular shape, bound warps (Fig. 1DD).

Method of work: weave from right to left.

Shaping: tension; adding warps (Fig. 2B).

Shape: rectangular; flanging quadrilateral; circular; half-oval.

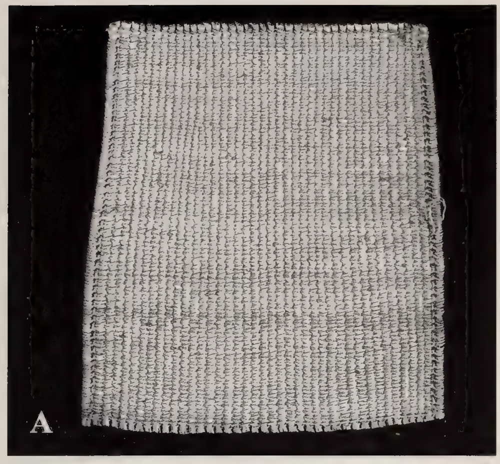
Edge: warp: wrapped (Fig. 2Q); half cut off, half tucked back to front to back and cut (Fig. 2I or J); half cut off, half to join last row of twine to look like plaiting of the last row (Fig. 2N); several rows of fine twine; row of wrapping, chain effect (Fig. 2R); elements tucked under last row of twine (Fig. 2G); weft: front weft wrapped over three, back weft over two, or across front warp and back (Fig. 2AA), last warp sometimes thickened.

Finishing: weft elements tied with a knot at start and end; in body of work just cut off.

Decoration: all over chain twine (Fig. 1I); alternating bands of plain and chain stitch (Fig. 3I); lines or diaper pattern by lengthening stroke (Fig. 3K); a raised line of three- strand twine (Fig. 3L); warp edge may be of different material, or different colour; three rows of lattice twine (Fig. 3J); bands of open twine; split warp on body of plain twine (Fig. 3G).

Ornamentation: none.

Utilitarian addition: loop of bark fibre thread for hanging.



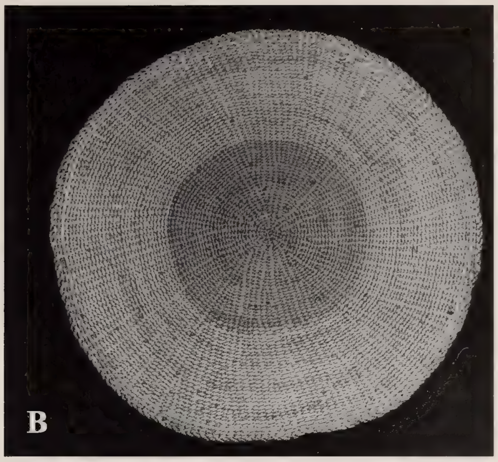
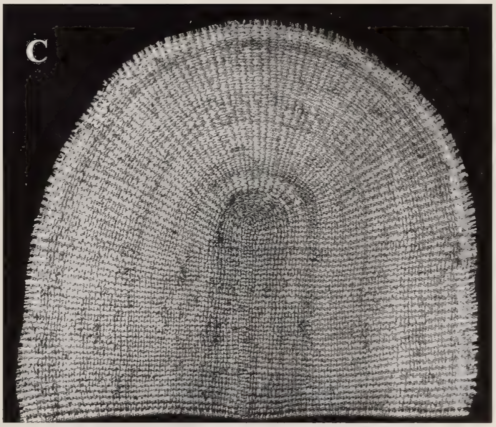
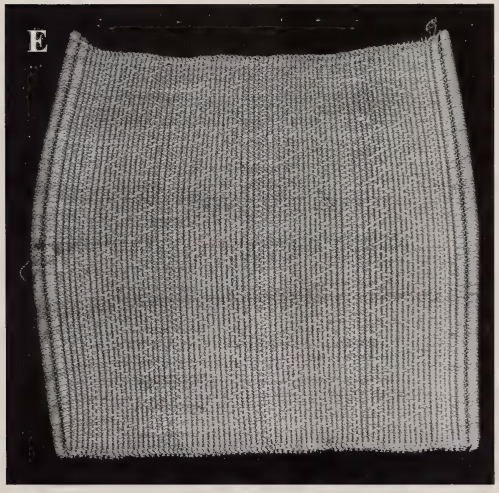


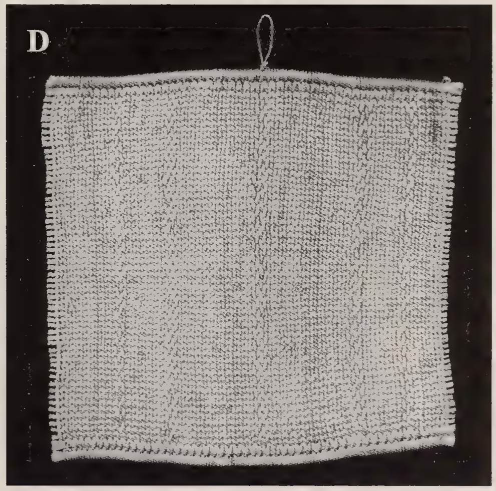
Figure 21

isithebe, food mat.

A. Mpondo, Lusikisiki, 1948. Length 364 mm. SAM–6683.
B. Mpondo, Libode, 1969. Diameter 330 mm. SAM–9564.
C. Mpondo, Libode, 1969. Length 570 mm. SAM–9553.
D. Nci, Izingolweni, Harding, 1969. Length 320 mm. SAM–8447.
E. Mpondomise, Tsolo, 1969. Length 515 mm. SAM–9578.







Tools

None.

Materials

Warp: thick sedge or grass

Weft: thin or coarse sedge.

The sedge is dried (Fig. 22), then the night before use it is left out in the dew.

Makers

Women.

Records

Early: Smith 1831–1832 [1955: 186], Mpondo. Döhne 1836–1844 [1844: 42], Xhosa. Kropf 1846–1889 [1889: 101], Xhosa.

Recent: Kidd 1904, pl. 79, Mpondo. Müller 1926: 41, Hlubi. Hunter 1936: 365, Mpondo. Duggan-Cronin 1949: 28, Mpondo. Hammond-Tooke 1963: 302–319, general. SAM–9653, Xhosa, King William's Town. Shaw & Van Warmelo 1981: 410, 417, 419, general. UCT–32/43, 1932, Mpondo, Flagstaff. SAM–5550, 1936, Mpondomise, Tsolo. SAM–6055, 1939, Mpondo, Libode. EL 993, Xesibe, Mount Ayliff.

Field survey: 1948: Mpondo, Lusikisiki, SAM–6683. 1961: Hlubi, Herschel, SAM–8528; Nci, Harding, SAM–8446, SAM–8447. 1968: Mpondomise, Tsolo. 1969: Mpondo, Libode, SAM–9553; Thembu, Engcobo; Mpondomise, Tsolo, SAM–9578; Mpondo, Mevana, Libode and Ngqeleni; Mfengu, Peddie. 1971: Xhosa, Kentani; Bhaca, Mount Frere. 1984: Mpondo, Libode, D & H. 1985: Xhosa, Willowvale, D & H.

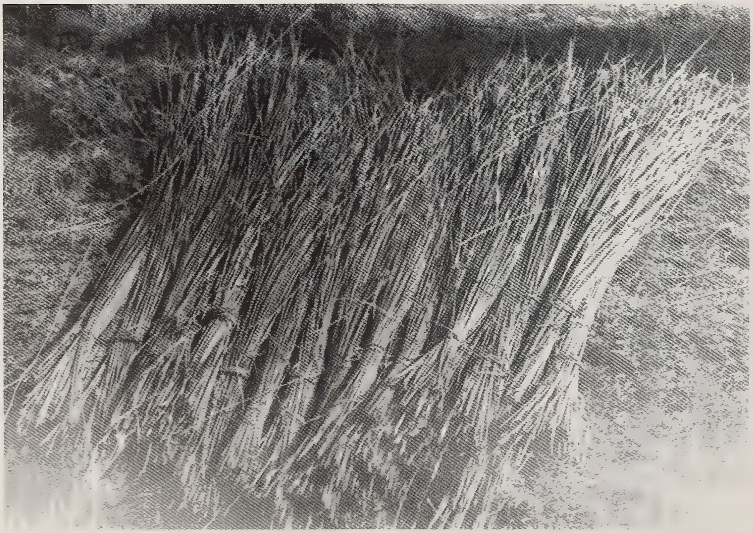


Figure 22

Small bundles of *Cyperus*, collected for making *isithebe*; Mpondo, Libode, D & H, 1984.

2. ***isixazi***: Xhosa; *ucango*: Bomvana; *uhlango*: Mpondo (Fig. 23); *isithebe senyama*: Xesibe. This is a wicker tray for sharing out raw meat or serving meat to men only. It was recorded only from the Xhosa, Bomvana, Mpondo and Xesibe. The same name is used by Bomvana for door (Fig. 39). Both are made in the same technique.

Techniques

Fabric: chequer wicker (Fig. 1O).

Beginning: warps laid side by side and held with weft (Fig. 1AA).

Method of work: not known.

Shaping: none.

Shape: rectangular; size seen at Lwandile, 60 x 45 cm.

Edges: warp: stapled (Fig. 2U); weft: weft element taken straight back into next row (Fig. 2W).

Finishing: none.

Decoration: none.

Ornamentation: none.

Tools

If any, not known.

Materials

Warp: slivers of wood (at Lwandile *ugonothi*).

Weft: creeper or crushed reed.

Makers

Men.

Records

Early: Maclean 1858: 155, Xhosa. Shaw 1820–1856 [1860: 368], Xhosa.

Recent: Cambridge 1934.112, Mpondo. Hunter 1936: 17, Mpondo. SAM–6091, 1939, Mpondo, Libode.

Field survey: 1969: Mpondo, Lwandile.

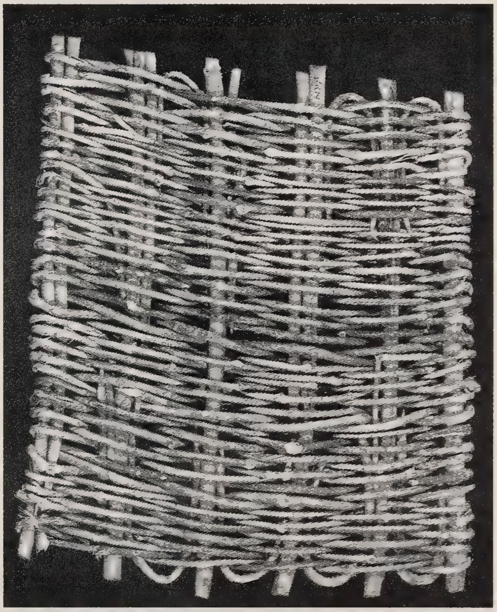


Figure 23

isixazi, tray for serving meat, Mpondo, Libode, 1936. Length 364 mm. SAM–6091.

STRAINERS AND SKIMMERS

During the process of making beer, after the initial fermentation, the liquid is strained by squeezing it through a strainer (Figs 24–28). The Bhaca also use small strainers for straining children's porridge. According to Alberti (1810), the Xhosa of his day used the nests of the weaver bird as strainers for beer. Skimmers (Fig. 29) are used to skim the scum or foreign objects off the surface of the beer when it is being served.

1. ***intluzo***: general except Bhaca; or *imijijwa*: Mpondo; *ivovo*: Bhaca. A long, funnel-shaped basket, closed at one end, and worked loosely for pliability. It is nearly always fitted with a loop for hanging (Figs 24–28).

Techniques

Fabric: i. *intluzo*, straight sewn, foundation elements twisted into two- or three-ply cord (Fig. 1V), general (Fig. 25).

ii. *intluzo*, open and close diagonal and zigzag split-warp twine (Fig. 1K–N), Thembu (Fig. 28).

iii. *ivovo*, Mpondo, Xesibe, Bhaca and Xolo only, diagonal twill (Fig. 1B) over three or four elements (Figs 24, 27).

iv. plain open twine (Fig. 1G), Bomvana.

Beginning: i. *intluzo*, foundation strands knotted and joined in a circle by the first row of work (Fig. 1CC), end of sewing strand may be worked in as foundation.

ii. *intluzo*, warps knotted and joined in a circle by the first row of work (Fig. 1AA).

iii. *ivovo*, knotted in pairs (Fig. 1BB).

iv. start with the plaited hanging loop and let the material of the loop become the warp.

Method of work: the sewn strainer is made on a core of grass, usually but not always, starting at the mouth (Figs 25, 26). The two- or three-ply foundation strands are twisted in preparation before the work begins.

Shaping: tension; elements threaded to inside, knotted and cut off inside tube (Fig. 2C); natural decrease of material.

Shape: tubular.

Edge: beginning forms edge, with knots cut short or left long enough to form a short fringe (Fig. 2T); several rows plain twine, then alternate warps cut (Fig. 2K), others from back to front to back; on twine, warps twisted and bent to right in front of next warp and

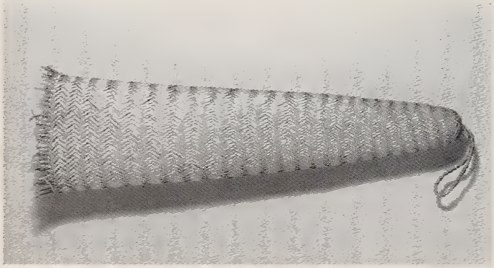


Figure 24 (*above*)

ivovo, beer strainer, Mpondo, Flagstaff, 1932. Length 630 mm. UCT–32/44.

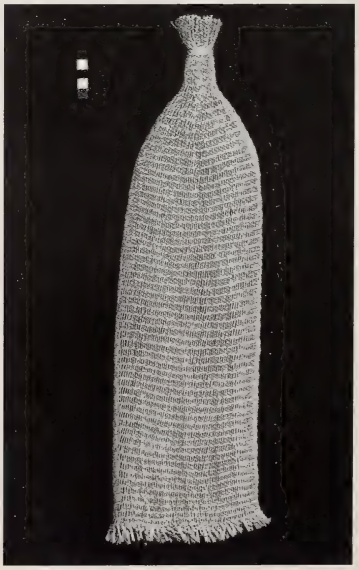


Figure 25 (*right*)

intluzo, beer strainer, Hlubi, Herschel, 1961. Length 880 mm. SAM–8566.

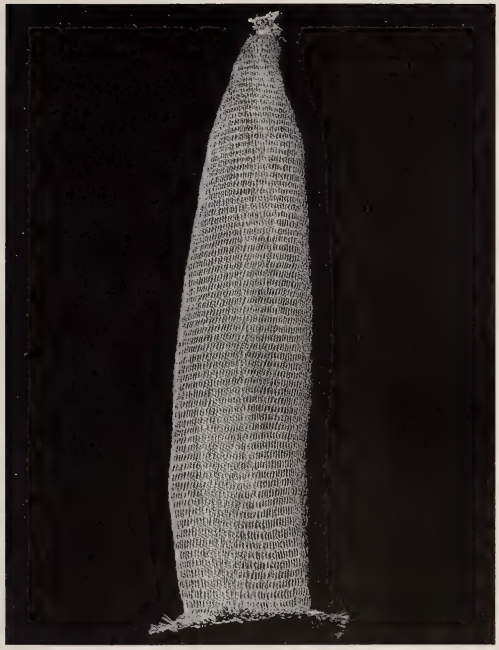
through to back (Fig. 2H); on twill, fringe below knots of beginning.

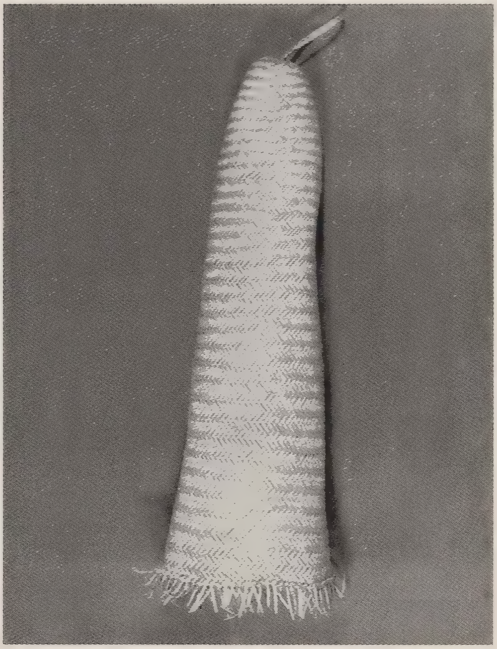
Finishing: spiny cone with hanging loop (Fig. 3D); ends bound together with bark cord to make a 25 mm knob; elements turned inside and hanging loop, which may be plaited, knotted with them (Fig. 3E).

Decoration: in the sewn variety, a vertical line or lines by a different ply or a different twist or direction of foundation (Fig. 3P); lengthening gap (Fig. 3Q); latterly, introduction of coloured strands, same material dyed (Fig. 3U).

Ornamentation: none.

Utilitarian addition: plaited or twisted loop for hanging.





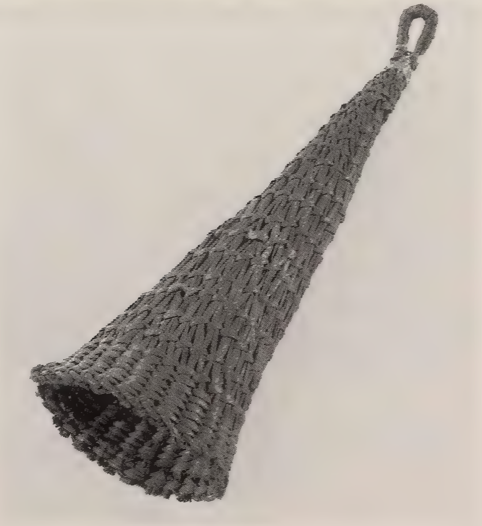


Figure 26 (*above*)

intluzo, beer strainer, Mpondomise, Tsolo, 1936. Length 565 mm. SAM–9576.

Figure 27 (*above right*)

ivovo, beer strainer, Xolo, Port Shepstone, 1939. Length 555 mm. SAM–6010.

Figure 28 (*right*)

intluzo, beer strainer, Thembu, Mqanduli, 1935. Length 228 mm. NCHM ET 35/357.

Tools

Core of grass to hold shape; for sewing, a plain or curved needle, *inhlambo* (Hlubi); a metal needle with a bone handle; formerly a wooden needle (Hlubi).

Materials

Foundation: i. two- or three-ply twisted cord of split sedge, gathered from the river, dried and then wetted and twisted for work. ii. split sedge. iii. split folioles of *Hyphaene coriacea* palm-leaves.

Sewing: i. two-ply cord of split sedge, dried after gathering, then wetted and twisted for work; or, latterly, grain-bag fibre. ii. split sedge. iii. split folioles of *Hyphaene coriacea* palm-leaves.

Makers

i, ii and iv (see above), women; iii. men.

Records

Early: Alberti 1803–1806 [1810: 36–40], Xhosa; Fritsch 1863–1866 [1872: 76], Xhosa.

Recent: Müller 1926: 41, Hlubi. Soga 1932: 399, 401, Xhosa. UCT–32/44, Mpondo, Flagstaff. NCHM ET 35/357, Thembu, Mqanduli, 1935. Hunter 1936: 99, Mpondo. SAM–4971, 1933, Thembu, Cala. SAM–5564, 1939, Mpondomise, Tsolo. SAM–6010, Xolo, 1939, Port Shepstone. SAM–6054, 1939, Mpondo, Libode. Shaw & Van Warmelo 1974: 213, pl. 30; 1981: 412, 436, pls 61–62.

Field survey: 1961: Hlubi, Herschel, SAM–8523; Hlubi, Quthing, SAM–8566. 1969: Thembu, Engcobo; Mpondomise, Tsolo, SAM–9576; Mpondo, Ngqeleni, SAM–9566; Bhaca, Mount Frere, SAM–9628. 1985: Xhosa, Willowvale (D & H).

2. ***isiketho***: Mpondo; *isihlenga*: Mpondo (Fig. 29). A woven spoon for removing scum or flies from the top of beer. This was recorded in the field only among the Mpondo of Lusikisiki. It has probably been borrowed from KwaZulu-Natal where such spoons are used.

Techniques

Fabric: warps bent at centre to form a bowl, held at wide intervals with double row of twining; warps bound or chequer woven together to form a single or double handle, with a ring or a loop at the end.

Materials

Warp and weft midribs of palm-leaf folioles.

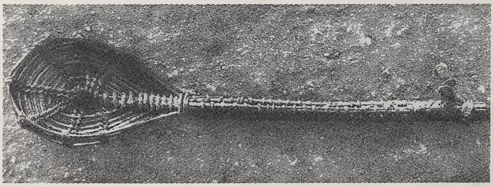


Figure 29

isiketho, skimming spoon, Mpondo, Lusikisiki, 1948. Length 210 mm. Photo N. J. van Warmelo.

Records

Early: Nil.

Recent: NCHM ET 35/426, 1935, Mpondo, Bizana. Shaw & Van Warmelo 1981: 424, 426, pl. 66.

Field survey: 1948: Mpondo, Lusikisiki.

3. ***isongulo***: Xhosa. This was described by informants as a skimmer with a woven head and a wooden handle. It was not seen.

FURNISHING MATS

Long rectangular mats were made in different sizes according to use. The longer were used as beds on which to sleep, and were rolled up and put on one side during the day. The shorter were used as children's beds or as sitting mats for many occasions. It was customary to take one's own mat when travelling. The mats might also serve as shrouds. Mats were also used to screen off part of the hut on special occasions, or to keep off the draught from the door. The coarser sort were used for laying out tobacco to sweat. Among the Mfengu of Peddie, where they were no longer used as beds, some were seen hung on the walls as ornaments.

1. ***ukhuko***: general, except Xesibe and Bhaca; *isicamba*: Mpondo; *icansi*: Xesibe, Bhaca, Hlubi, Mfengu; *isicangca*: Xhosa, Bomvana, Mpondo, Xesibe. A sleeping mat; according to Thembu this is the twined variety (Fig. 30).

2. ***isicamba***: Xhosa, Mpondo; *isicangca*: Xhosa, Bomvana, Xesibe, Mpondo; *isihlalo*: Xesibe. A smaller sleeping mat or sitting mat.

3. ***umahambehlala***: Xhosa, Mpondo, Bhaca, Hlubi, also called *moseme*, from the Sotho. A special sitting mat, especially for women, and especially when nursing a baby.

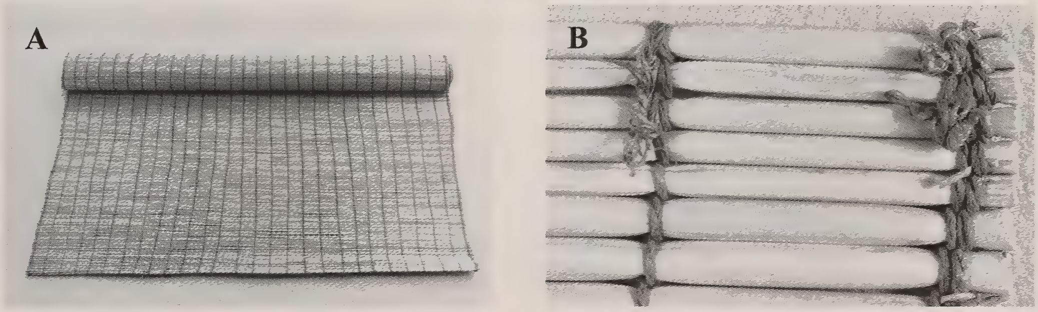


Figure 30

ukhuko, *isicamba*, *ucansi*, *isicangca*, sleeping mat.
A. Mpondomise, Tsolo, 1936. Length 2 215 mm, width 1 150 mm. SAM–5565.
B. Close-up of SAM–5565, showing twined technique and edge.

4. ***isigcobo***: general. A rough mat for babies to sleep on and for many other purposes, including sweating tobacco (Fig. 31).

5. ***nqoboko***: a sewn sleeping mat, Thembu, Hlubi (Herschel), 1961.

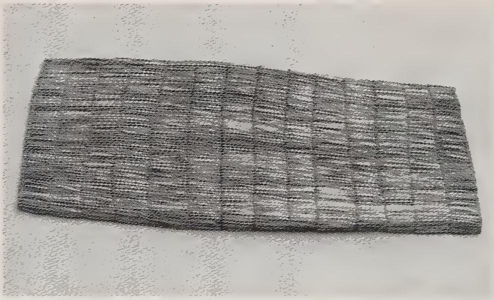


Figure 31

isigcobo, rough mat for sweating tobacco, Mpondo, Libode, 1939.
Length 1 525 mm, width 750 mm. SAM–6060.

Techniques

Fabric: open twine over single or multiple warp (Fig. 1G, H); a small number – five out of the 45 seen – were straight sewn (Fig. 1U).

Beginning: lay warps flat and hold by first row of weft or sewing (Fig. 1AA).

Method of work: the material is worked wet.

Shaping: none.

Shape: rectangular.

Edge: warp – double row of close twining (Fig. 2O, P); one row twine, one row wrapping under one and over two (Fig. 2Q); wrapping under two over three; scalloped; weft: back in tracks over one or two warps (Fig. 2V); carried down taut to re-start (Fig. 2X); zigzag twining between rows (Fig. 2Y); wound round last two elements (Fig. 2Z).

Finishing: weft elements – ends oversewn; ends knotted at edge.

Decoration: twining in pattern between rows of open twine (Fig. 3H); rows of crossed warp (Fig. 3N).

Ornamentation: none.

Tools

For twined work only a cutting tool is needed for trimming; for sewn work Hlubi and Xhosa of Herschel use an awl to open the hole in the wet material, then push a needle through while the awl is still in position (the Khoekhoe method); a sailmaker's needle is also used today.

Materials

Warp and foundation elements: sedge, of different qualities according to use (Kay 1833: 147). Bhaca import it by lorry from East London. Bullrush leaves for rougher mats.

Weft and sewing strand: sinew (Von Winkelman 1788–1789 [1932: 84]), two-ply cord of bark fibre, grain-bag twine, sisal fibre, thin strips of bark or string.

Makers

Women.

Records

Early: Von Winkelman 1788–1789 [1932: 76, 84], Xhosa. Alberti 1803–1806 [1810: 48], Xhosa. Kay 1827 [1833: 147], Xhosa. Smith 1831–1832 [1955: 186], Mpondo. Döhne 1836–1844 [1844: 29, 42–44], Xhosa. Backhouse 1839 [1844: 270], Mpondo. Kretzschmar 1853: 239, Xhosa. Maclean 1858: 162, Xhosa.

Recent: Bachmann 1901: 164, Mpondo. Kidd 1904: 314, Mpondo. Müller 1926: 41, Hlubi. Cook 1931: 67, Bomvana. Soga 1932: 217, 231, Xhosa. UCT–32/46, 1932, Mpondo, Flagstaff. SAM–5565, 1936, Mpondomise, Tsolo. SAM–6056, SAM–6060, 1939, Mpondo, Libode. SAM–6089, 1939, Nzimakwe, Port Shepstone. Brownlee 1944: 24, Xhosa. Hunter 1936: 87, Mpondo. Broster 1967: 131, Thembu. Tyrrell 1968: 192, 194, Xhosa. Shaw & Van Warmelo 1981: 378–380; 1988: 744, general.

Field survey: 1948: Mpondo, Qawukeni. 1961: Vundla, Quthing; Hlubi, Herschel, SAM–8565; Hlubi, Matatiele; Mfengu, Peddie. 1968: Xhosa, King William's Town, SAM–9424; Bhaca, Mount Frere. 1969: Xhosa, Kentani.

FISH-TRAPS

In the main, the Southern Nguni were not fish-eaters. The only two basket traps recorded were used by the coastal Bomvana and Mpondo.

1. ***uzwazwa***: Mpondo. A bag-shaped basket made of sedge in a very open twine (Fig. 1G). It is used for catching shrimps or fish by holding it behind the retreating wave and letting the water run through it. It was used by Mpondo and Bomvana (Fig. 17). The term was also used for a fixed conical fish-trap, according to an isolated, unconfirmed report from informants at Mbotye Bay.

Techniques

Fabric: open zigzag split-warp twine (Fig. 1L), Bomvana; open twine (Fig. 1G), rows closer at base to prevent escape of the catch, Mpondo.

Beginning: warps joined at centre with one row of weft (Fig. 1AA) and bent up.

Method of work: not known.

Shaping: none.

Shape: rectangular.

Edge: three rows of close twine in opposite direction to open twine (Fig. 2P); warps cut off a centimetre above this.

Finishing: ends cut off.

Decoration: none.

Ornamentation: none.

Utilitarian addition: handle.

Tools

Not known.

Materials

Thick-stemmed sedge.

Makers

Not known, but likely to be women.

Records

Early: Nil.
Recent: MM 1822, Bomvana. SAM–6057, Mpondo, Umvume Springs.
Field survey: 1948: Mpondo, Mbotye Bay.

SLEDGES

1. ***isileyi***: general (Fig. 32). The sledge is a modern innovation. It is hitched to oxen to convey produce from the fields or to transport any heavy material. Strong wooden stakes are planted in a heavy forked wooden base to serve as warps. The walls are completed with pliable wooden wefts and the base filled in with a wicker floor, or latterly with wooden planks (see no. 1 in Materials below). A variety (see no. 2 in Materials below) in which the walls consisted of coiled sewn maize stalks was seen among the Thembu near

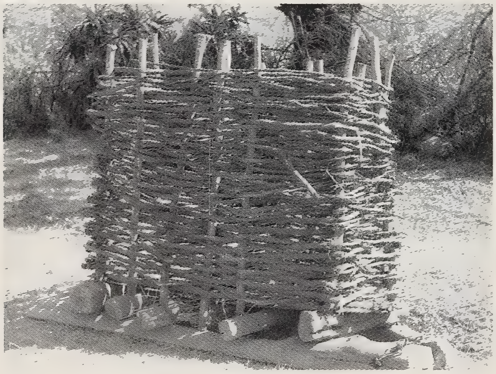
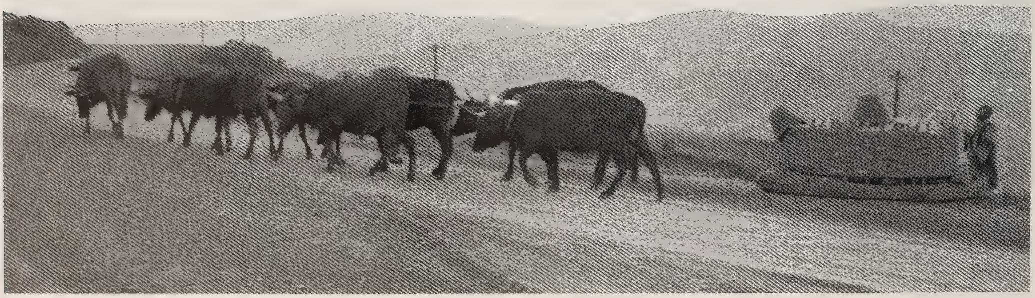


Figure 32

isileyi, sledge.
A. (*left*) Xesibe, Mount Ayliff, 1969.
B. (*below*) Mpondo, on the road near Lusikisiki, 1971.



Engcobo, and Bhaca spoke of the upper part of a sledge being 'basketwork'. Sledges were seldom seen by the late 1990s.

Techniques

Fabric: chequer wattle (Fig. 1P); simple oversewing on coiled foundation (Fig. 1X).
Beginning: warps stuck into the base.
Shaping: position of warps.
Shape: triangular base, sometimes flanging walls.
Edge: sometimes stapled (Fig. 2U).
Finishing: none.
Decoration: none.
Ornamentation: none.

Tools

Not known.

Materials

Base: a forked tree trunk or two thick wooden logs.

Walls: 1. *warps:* wooden stakes; *wefts:* pliable stems of tecoma (*Tecomaria capensis* Spach), *isithombothi* (*Acalypha glabrata* Thunb.), *umhlali* or *uzungo* (*Rhoicissus rhomboidea* (E. Mey) Planch.)

2. *foundation:* maize stalks; *sewing:* bark or split withies.

Makers

Men.

Records

Early: Nil.

Recent: Hunter 1936: 88, Mpondo. Walton 1954: 24, general. Shaw & Van Warmelo 1974, pl. 25 (fig. 3), pl. 33 (figs 3–4), Xhosa, general; 1981: 238, general.

Field survey: 1961: Bhaca, Mount Frere; Hlubi, Herschel. 1968: Mpondo, Mgazana Mouth. 1969: Xhosa, Kentani; Thembu, Engcobo; Mpondo, Mevana; Xesibe, Mount Ayliff. 1971: Mpondo, Libode. 1985: Mpondo, Libode (D & H).

BUILDING TECHNIQUES

Before sun-dried mud bricks and modern structures took over, some wattlework was used, especially in the east of the area, in building the framework of hut walls. Fences, including those for cattle enclosures, fowl-coops and open-air granaries were also built in this technique, the latter mainly in the west.

1. ***uphahla***: Mpondo. Frame for the wall of a cylindrical hut (Fig. 33).

Seen in the eastern part of the area only and said to have been introduced there in the

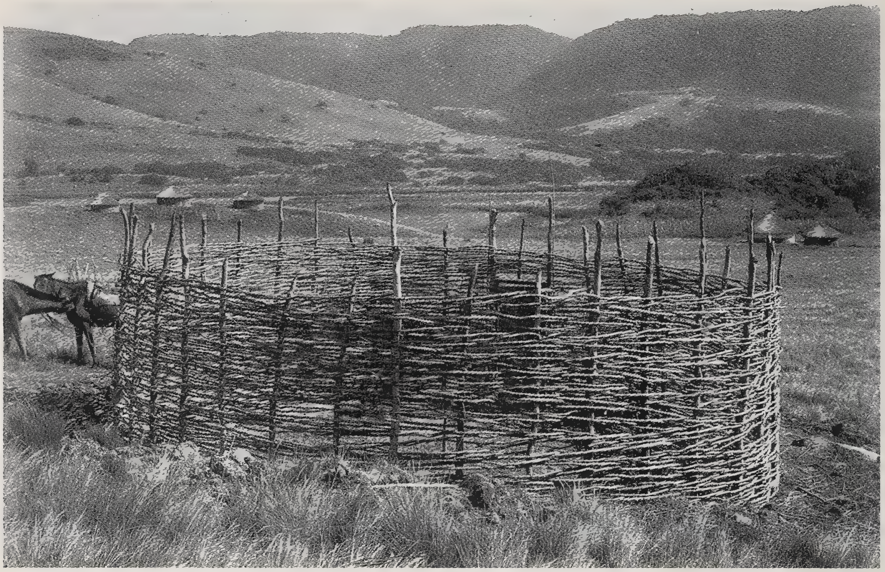


Figure 33

uphahla, hut frame, Mpondo, Mbotye, 1948. Photo N. J. van Warmelo.

mid-nineteenth century. Strong saplings are planted in a circle as warps and thinner sapling wefts are woven into them in chequer weave. On the frame of the old-style huts the side pieces were not woven, but tied, to the vertical posts. This word is now generally used for the roof of a stone-walled hut.

In the west, the roof thatch was held down by plaited ropes – one set, the warps, fastened at intervals from the top to the edge, and the other set, the wefts, wrapping round them, making rows of open wrapping (Fig. 1C).

2. ***inyango***: Xhosa, Mfengu. Formerly a small store hut on poles, now an ordinary store hut (Fig. 34).

3. ***ingobe***: Mpondo. Temporary rough hut of bent saplings for use while a permanent hut is being made.

4. ***udladla***: Xhosa, eastern Mpondo, Xesibe, Bhaca (Fig. 35). Open-air granary in the shape of a tall cylinder, for storing maize, generally having a small door at the base. The warps are long saplings planted in the ground in a circle. The wefts are thinner saplings and the weave is chequer. This is an article typical of the western part of the Eastern Cape, but has been seen in the east. One seen in Kentani in 1969 had the lower section covered with clay and the inside lined with palm-leaves.

5. ***ubuhlanti***, *isibaya*: general. Enclosure for cattle or small stock (Fig. 36).

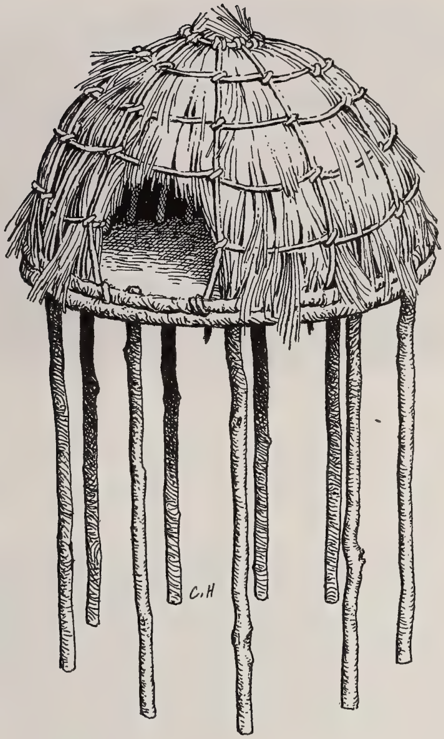


Figure 34

inyango, store, 'Kafir' (Xhosa), 'Kafirland'. After Graham, L. & Robinson, H. (1854).

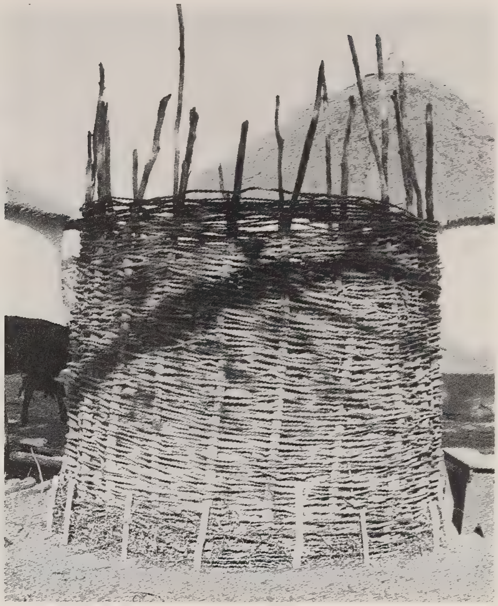
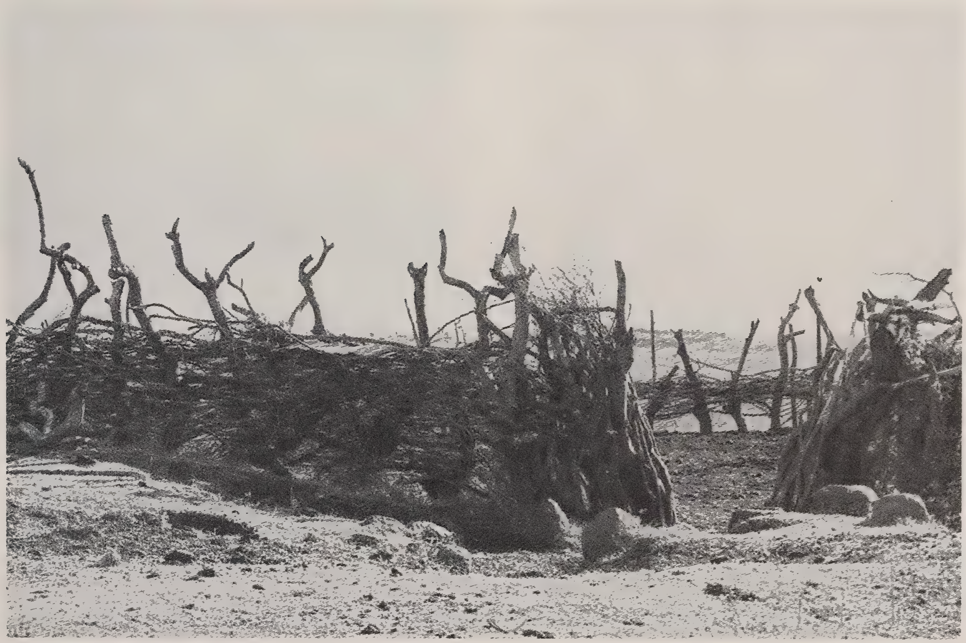


Figure 35

udladla, open storage bin, Xhosa, Willowvale, D & H 1985.

Figure 36 (*below*)

ubuhlanti, cattle enclosure, Mpondo, Libode, D & H 1985.



6. ***indlwana yenkuku***: general. Small fowl-coop, similar in structure to a granary, but roofed. Some have a short, roofed passage to the door (Fig. 37). Individual nests are made on a forked stick and fixed against the wall inside the hut (Fig. 38) (Davison & Hooper pers. comm. 1984).

7. ***uthango***, *ujilo*: Xhosa, Bomvana; *impingelo*: Bomvana. Wattlework fences. Poles are planted in the ground and pliable saplings are woven in close or open chequer weave. Such fences were used for cattle enclosures as well as gardens, screens (*ikhusi*) inside the hut and traps. They used to be renewed each year, but for a long time there has not been enough wood.

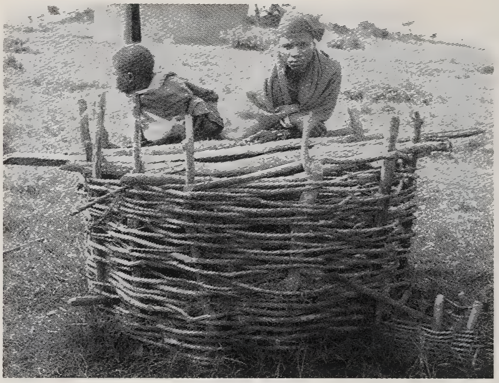


Figure 37

indlwana yenkuku, chicken coop, Bomvana, Elliotdale, 1948.
Photo N. J. van Warmelo.

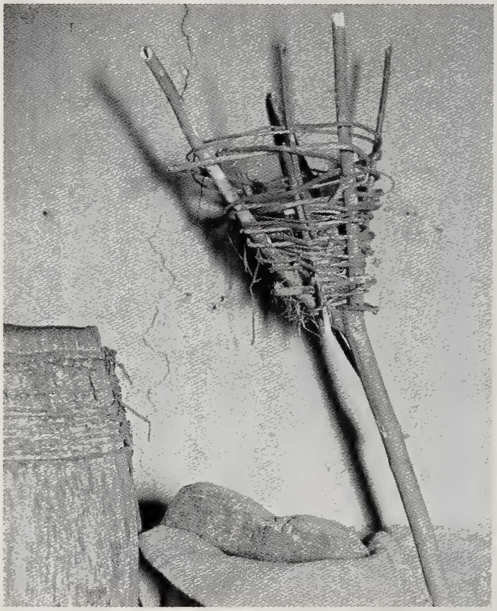


Figure 38

Nest, Mpondo, Libode, D & H 1984.

Techniques

Fabric: close or open chequer or twined wattlework (Fig. 1P).

Beginning: warp, sticks planted in the ground; or a forked stick (Fig. 36).

Shaping: placing of warps; bending of warps for fowl-coop roof.

Shapes: cylindrical; conical; straight.

Edge: none.

Finishing: none.

Decoration: none.

Ornamentation: none.

Tools

An axe for cutting the material.

Materials

Wooden stakes and withies or creepers, *igonoti* plant (Bomvana).

Makers

Men.

Records

Early: Van der Kemp 1799–1806 [1806: 437], Xhosa. Alberti 1803–1806 [1810:

104–5], Xhosa. Smith 1831–1832 [1955: 108], Mpondo. Kay 1827 [1833: 117, 129, 362], Xhosa, Mpondo. Morgan 1833: 34, Xhosa. Baines 1849 [1961: 169], Xhosa, Mfengu. Shaw 1820–1856 [1860: 387], Xhosa. Bonatz 1834: 308, Thembu. Backhouse 1839 [1844: 236], Xhosa. Kropf 1846–1889 [1889: 99], Xhosa.

Recent: Scully 1901: 43, Hlubi. Kidd 1904: pl. 93, Mpondo. Müller 1926: 20–21, Hlubi. Cook 1931: 158, Bomvana. Soga 1932: 409, Xhosa. Hunter 1936: 97, Mpondo. Shaw & Van Warmelo 1972: 70, 72, 83, 84, 98, pl. 5, pl. 12 (fig. 1), pl. 14, Xhosa, Mpondo, pl. 15, Xhosa, Mpondo, pl. 17 (fig. 2), Xhosa; 1974: 163, general. EL Eth. 5317, Bomvana, 1969.

Field survey: 1968, 1969: Mpondo, Libode. 1971: Xhosa, Kentani. 1984: Mpondo, Libode, SAM–12722 (D & H).

8. ***ucango***: Xhosa; *uhlango*: Mpondo, Xesibe; *uhlako*: Bhaca. Doors of wicker chequer were used on the old grass huts and many modern huts. The door was a rectangular structure of thick withies, woven chequer, and it was sometimes plastered with mud (Fig. 39). It was held in position across the doorway by a pole attached to its centre with rope. Some, possibly old ones, were used as part of the gate of the cattle enclosure.

Techniques

Fabric: chequer wicker (Fig. 1O).

Beginning: warps held by first row of weft (Fig. 1AA).

Shaping: none.

Shape: rectangular.

Edge: warps turn over into next gap; wefts turn straight back into next row (Fig. 2W).

Finishing: none.

Decoration: none.

Ornamentation: none.

Tools

Axe for cutting material.

Materials

Withies.

Makers

Men.

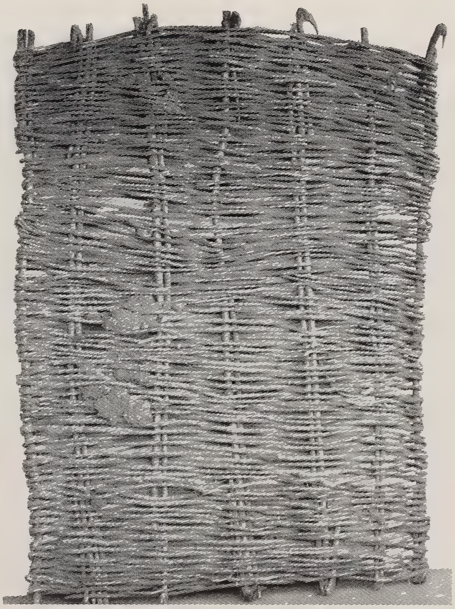


Figure 39

ucango, door, Mpondo, Libode, 1967.
Height 1 728 mm. MM no number.

Records

Early: Swellengrebel 1776 [Hallema 1932: 13], Xhosa. Smith 1831–1832 [1955: 167], Mpondo. Alexander 1835 [1837: 392], Xhosa. Shaw 1820–1856 [1860: 412], Xhosa. Fritsch 1863–1866 [1872: 77], Xhosa. Kropf 1846–1889 [1889: 98], Xhosa.

Recent: Cook 1931: 161, Bomvana. Shaw & Van Warmelo 1972: 70, general, pl. 9, Mpondo.

Field survey: 1948–1969: general. 1961: Mfengu, Peddie; Bhaca, Mount Frere.

CLOTHING AND ORNAMENT

CEREMONIAL COSTUME

1. ***umhlambi***: a palm-leaf dancing skirt (Fig. 40); *ingcambeni*, a palm-leaf head-dress; a veil of rush or palm-leaf.

2. ***iphunga***: a palm-leaf veil for the face; palm-leaf arm-bands and leg-bands. These items make up the costume worn by the newly-circumcised initiates (*abakhwetha*) for the dancing that ends the initiation period (Fig. 41). Each is a fringe of palm-leaf (*Phoenix reclinata* Jacq.) of different lengths and split to different widths according to the item, and held at one edge by one or two rows of wrapping or lattice wrapping with a strip of bark. Each has ties of two-ply bark cord except the skirt, which has a plaited bark waist-string. Bomvana fathers have to travel some distance to obtain the material, as the *Phoenix* palm does not grow in Bomvanaland. Mfengu and Hlubi hold initiation schools, but no record has been made of any special dress. Other eastern people may have held the schools in the past, but have not done so for a very long time.

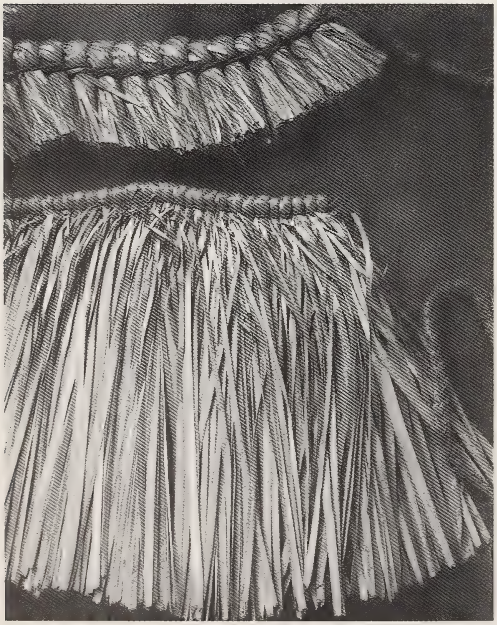


Figure 40

Detail of *umhlambi,* a *khwetha* initiate's skirt, Bomvana, Elliotdale, 1935. NCHM ET 35/838. Photo N. J. van Warmelo.

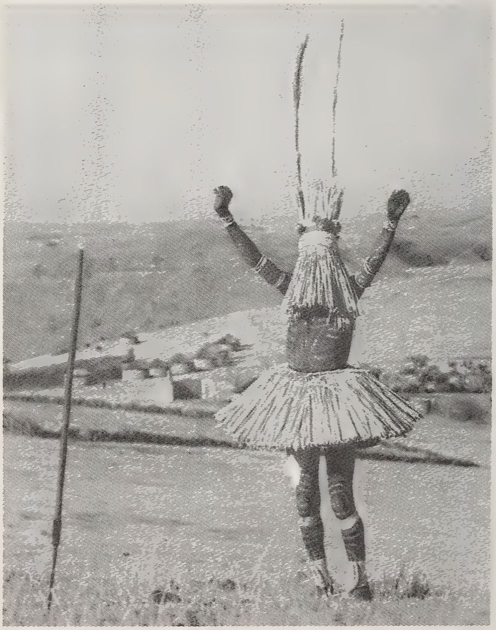


Figure 41

khwetha, initiate, Eastern Cape, *c.*1920. Photo Transkei Studio.

Techniques

Fabric: double row of wrapping (Fig. 1C) for skirt; single row of lattice-wrap (Fig. 1D) for accessories.

Beginning: the first bunch of fringe is held by the wrapping (Fig. 1AA).

Method of work: not known.

Shaping: cut where needed.

Shape: skirt: an increasing depth of fringe; accessories: rectangular.

Edge: none.

Finishing: knotted.

Decoration: none.

Ornamentation: none.

Tools

Not known.

Materials

Leaf of palm, *Phoenix reclinata* Jacq.; bark fibre for cord.

Makers

Men (the fathers of the initiates).

Records

Early: D'Almada 1622 [1902: 92], Xhosa. Von Winkelman 1788–1789 [1932: 89], Xhosa. Kay 1827 [1833: 76], Xhosa. Morgan 1833: 38, Xhosa. Shaw 1820–1856 [1860: 456], Xhosa. Kropf 1846–1889 [1889: 125], Xhosa.

Recent: SAM–665, 1907, Xhosa. Cook 1927: 60–61, Bomvana. Brownlee 1928: 180, Mfengu. UCT–29/1, 29/2, 29/33, 1929, Xhosa. Soga 1932: 255–256, Xhosa. NCHM ET 35/838, Bomvana, Elliotdale, 1935. Duggan-Cronin 1939, pl. 32, Xhosa. Tyrrell 1968: 190, Xhosa. Gitywa 1971: 117, Xhosa. Shaw & Van Warmelo 1974: 163, pl. 32 (fig. 1), Xhosa.

Field survey: Nil.

OTHER RITUAL DRESS

1. 'Straw caps' are said to have been worn as charms by Mpondo twins (Schapera 1926: 126).

2. There are early accounts that when a widow left the homestead for the period of mourning for her husband, she returned 'clad only in a covering of woven grass' (Shaw & Van Warmelo 1988: 554). There is no detailed information about this costume.

ORDINARY DRESS

1. ***intshinga***: Thembu only. A boater-shaped hat worn formerly by young Thembu men as an ornament. It had a wide brim and a very small crown.

2. ***umnqwazi***: Thembu, Hlubi. The common variety of hat, worn by Thembu, Mpondo, Mpondomise and Hlubi herdboys (Fig. 42). It has a normal crown and a narrow brim. The Hlubi make another variety too, with a slightly arched crown and a sloping brim, but some of them have also adopted the conical shape of their Sotho neighbours.

Techniques

Fabric: coiled multiple foundation, simple, beeskep or furcate sewing (Fig. 1X, Y, Z); plain close twine (Fig. 1E).

Beginning: closed hole; bent foundation (Fig. 1GG).

Method of work: according to some, worked while material is green.

Shaping: placing of coil (Fig. 2D); adding extra warps (Fig. 2B).

Shape: boater, modified boater, inverted cone (Hlubi).

Edge: no edge; cross stitch; herring-bone; bound with tape or material.

Finishing: ends cut off in the fabric.

Decoration: use of horse hair on some.

Ornamentation: fine chain, leather, coloured braid, green wool.

Tools

An awl or wooden needle (Hlubi) or a thorn, for the sewn work.

Materials

Foundation: grass.

Sewing: grass or sedge.

Makers

Men and boys.

Records

Early: Von Winkelman 1788–1789 [1932: 85], Xhosa.

Recent: SAM–987, 1903, Thembu, Herschel. Müller 1926: 30, Hlubi. SAM–6062,

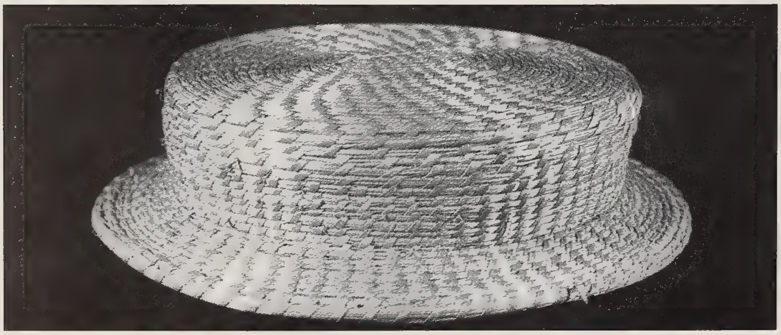


Figure 42

umnqwazi, herdboy's hat, 1939, Mpondo, Libode. Depth of crown 55 mm. SAM–6062.

1939, Mpondo, Libode. Shaw & Van Warmelo 1974, pl. 32 (fig. 2); 1988: pl. 78 (fig. 4), Thembu, Umtata.

Field survey: 1961: Hlubi, Herschel.

3. ***incitsho***: Bhaca. A sheath for the penis. Worn by circumcised men. Mount Frere, 1948 (Fig. 43).

Techniques

Fabric: plain close twine.
Beginning: not known.
Method of work: not known.
Shaping: flanging for first few centimetres then narrowing slightly to edge.
Shape: tubular.
Edge: warps bent straight back over plain row of material under two rows of weft.
Finishing: ends of warps cut off closely.
Decoration: three horizontal bands, same material, different colour.
Ornamentation: none.

4. ***ibhanti womdlezana***: Thembu; *isingqombo*: Qwati (Thembu). A belt to support a woman's stomach after confinement. It is said also to be worn as an ornament in front by women and behind by children.

Techniques

Fabric: straight sewn at wide intervals (Fig. 1W).
Beginning: bent foundation (Fig. 1GG).
Method of work: not known.
Shaping: placing of foundation coil (Fig. 2D).
Shape: long oval.
Edge: none.
Finishing: bound at the ends.
Decoration: none; use of coloured wool for sewing; beads.
Ornamentation: none.

Tools

Not known.

Materials

Foundation: grass.
Sewing: three-ply fibre cord; wool.

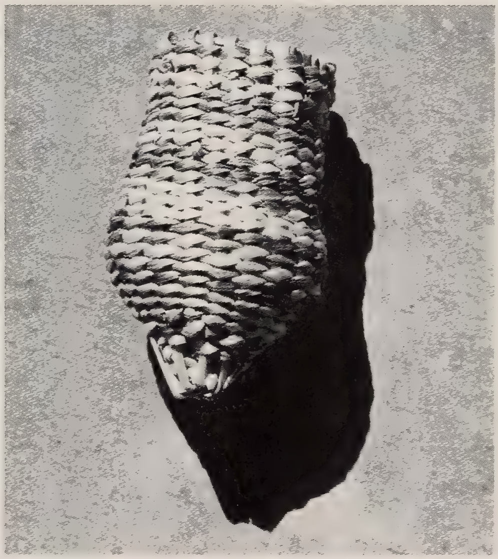


Figure 43

incitsho, penis-sheath, Mpondo, Lusikisiki, 1948. Length 49 mm.
Photo N. J. van Warmelo.

Records

Early: Nil.

Recent: Louw 1964: 11, Mpondo, Port St Johns. Shaw & Van Warmelo 1988: 544, general.

Field survey: 1969: Qwati (Thembu), Qebe Valley, SAM–9597.

ORNAMENTS

1. ***inquma***: a headband of a Xhosa headman. It was made of monkey-hair warps twined into a flat band with sinew thread wefts (Shaw & Van Warmelo 1988: 658, pl. 97 (fig. 3). It has also been recorded among the Thembu, NCHM ET 35/347 (Fig. 44).

Techniques

Fabric: two or three rows of close twine to form a narrow band.

Edge: none.

Finishing: ends joined to form a circlet.

Materials

Warps: fine monkey hair.

Wefts: sinew.

Records

Early: Nil.

Recent: NCHM ET 35/347, 1935; Shaw & Van Warmelo 1988: 658, pl. 97 (fig. 3), Xhosa.

Field survey: Nil.

2. In the late summer and autumn, when the grass is ripe, it has always been general custom throughout to make and wear a large number of necklaces, bangles, bandoliers and girdles (Fig. 46). The shiny flowering stalks of grasses of *Digitaria* spp., *umphica*, and others are used.

A variety of plaits is used and the ornaments appear to be named according to the type of grass or the type of plait used rather than to the object made. Later fashion has seemed to favour narrow strands, but older examples are often wide flat bands, or groups of flat, round, or square plaits (Fig. 1Q, R, S) sewn together at intervals or made into a fabric by straight sewing (Fig. 45). Some are decorated with beads (Fig. 3Y).

Techniques

Fabric: a variety of plaits (Fig. 1Q–S). Sometimes plaits are sewn together in bunches or as a flat fabric.

Beginning: a knot.

Method of work: made while grass is green (Thembu).

Edge: none.

Finishing: ends laid together with half-hitches (Fig. 3C) or spiny cone (Fig. 3D).

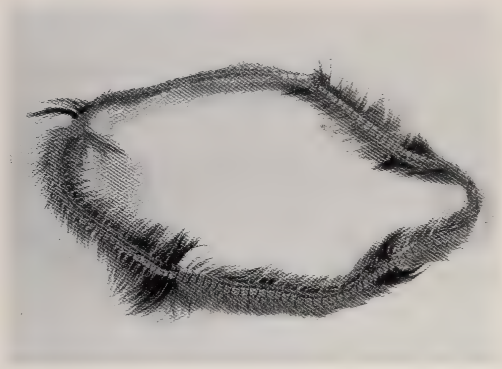


Figure 44

inquma, twined headband, Thembu, Mqanduli, 1935. NCHM ET 35/347.

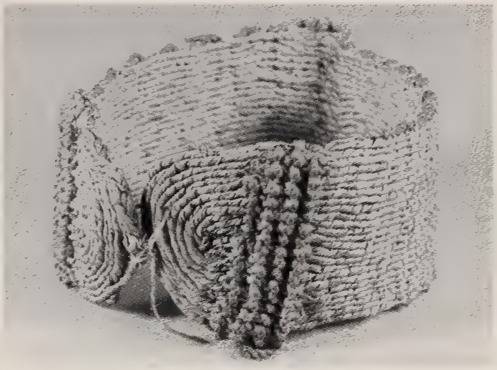


Figure 45

ibande, arm-band, ?Mpondo. Depth 55 mm. SAM–3355.

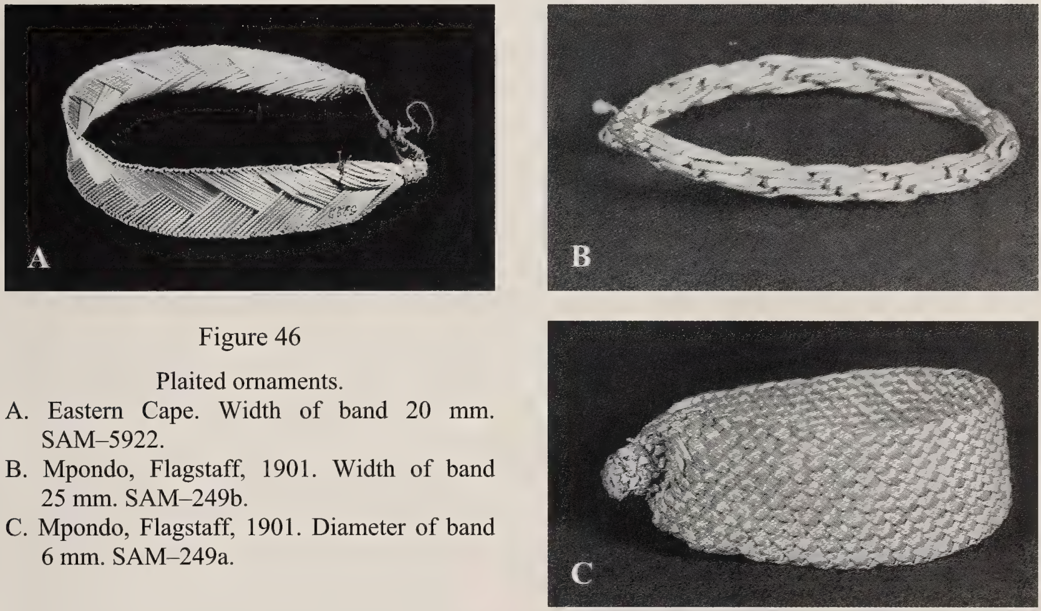


Figure 46

Plaited ornaments.

A. Eastern Cape. Width of band 20 mm. SAM–5922.
B. Mpondo, Flagstaff, 1901. Width of band 25 mm. SAM–249b.
C. Mpondo, Flagstaff, 1901. Diameter of band 6 mm. SAM–249a.

Decoration: some have beads added.

Ornamentation: brass buttons.

Tools

None.

Materials

Flowering stalks of grasses, mainly *Digitaria* spp., or very thin or stripped sedge.

Records

Early: Backhouse 1839 [1844: 269], Mpondo. Döhne 1836–1844 [1844: 42], Xhosa.

Recent: SAM–249, 1901, Mpondo, Flagstaff. TM 35/353, TM 35/360, TM 35/419, 1935, Bomvana. SAM–5922, 1938, Eastern Cape. SAM–8325, 1961, Thembu, Mqanduli. SAM–8634, 1948, Mpondo, Lusikisiki. Tyrrell 1968: 152, 154, 156, Bhaca. Gitywa 1971: 117–129, Xhosa.

Field survey: 1948: general, Eastern Cape. 1961: Thembu, Herschel, SAM–8534. 1969: Mpondo, Libode, SAM–9556.

MISCELLANEOUS

1. ***umtshayelo***: general, a broom (Fig. 47). Not all but many brooms are made of a bundle of grass or sedge stems, turned over and bound at one end with plaited horse hair, sedge cord, cord made from grass stems or grain- or orange-bag fibre, store-bought string or coloured cloth, to form a grip. The binding may pass over and under the outer grass stems in a simple or patterned chequer weave, or the thread may be sewn through the head. An alternative end is the spiny cone (Fig. 3D). In a fourth variety, the strands of the broom are joined together at one end by a row of twining to form a fringe that is then rolled up and bound at the grip to form the broom. In certain areas, for example in east Mpondoland, makers are more particular than elsewhere about the style of their brooms.

Techniques

Fabric: binding; chequer weave (Fig. 1A); spiny cone (Fig. 3D); simple twine (Fig. 1E); seizing; sewing through.

Decoration: none, other than the main technique, which may be decorative.

Ornamentation: sewn embroidery (Fig. 3X).

Tools

A needle to finish off the handle; shears to trim.

Materials

Warps (i.e. the strands of the broom): grass, sedge.

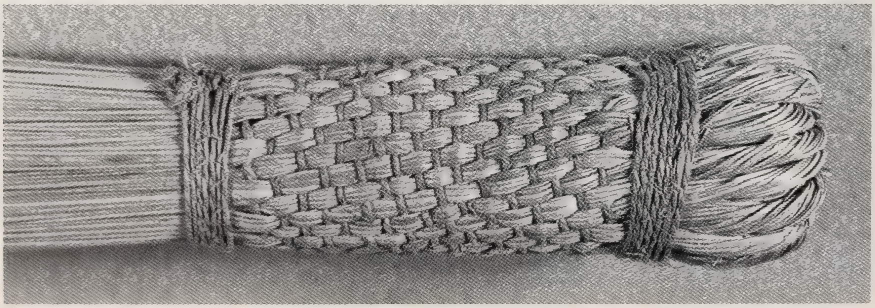


Figure 47

umtshayelo, broom, Mpondomise, Tsolo, 1935. Total length 510 mm. SAM–5508.

Weft: sedge, twisted bark strands, plaited horse hair, jute fibre, fine string, or cloth for binding.

Makers

Women generally, but one old man was seen in Mpondoland (D & H pers. comm. 1984).

Records

Early: Nil.

Recent: SAM–5508, 1935, Mpondomise, Tsolo. SAM–5551, 1936, Mpondomise, Tsolo. SAM–6061, 1939, Mpondo, Libode.

Field survey: 1961: Xhosa, Thembu, Hlubi, Herschel; Bhaca, Mount Frere. 1961: Thembu, Herschel, SAM–8557. 1969: Thembu, Engcobo; Mpondo, Libode; Mpondomise, Tsolo; Xesibe, Mount Ayliff. 1971: Mfengu, Sotho Location.

2. ***umichale***: Hlubi. A bridle made of a four-strand plait of the bullock's own tail hairs or of grass. It is passed through the beast's nose (Fig. 48).

Records

Early: Walker 1851 (*in* Backhouse & Tylor 1862, pl. 15), Xhosa.

Recent: Müller 1926: 10, Hlubi. Shaw & Van Warmelo 1981: 262, Hlubi, pl. 37 (fig. 2), Xhosa.

Field survey: 1961: Hlubi, Matatiele. 1969: Bhaca, Mount Frere.

3. ***isicheme***: a muzzle. A muzzle made of sedge and presumably woven, was put on to calves to prevent them from sucking.

Records

Early: Nil.

Recent: Shaw & Van Warmelo 1981: 262, general.

Field survey: 1948: Bomvana, Elliotdale.

4. **Stick covering**. The shaft of a dancing stick may be covered with a chequer weave (Fig. 1A) of sedge warp and string weft (Fig. 49).

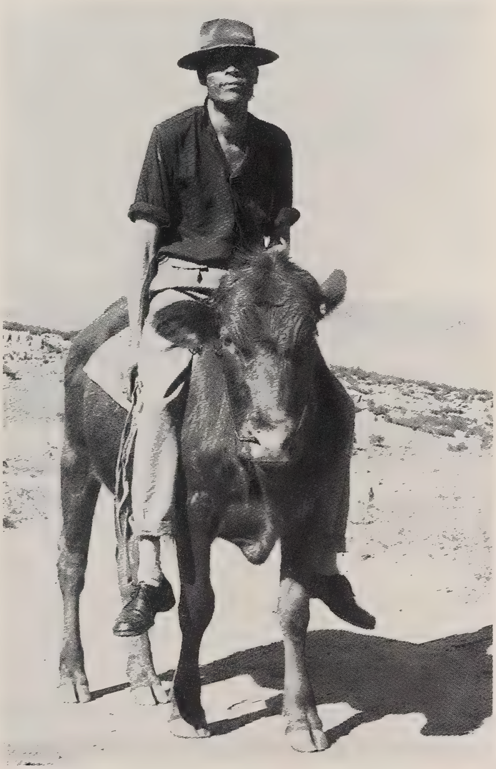


Figure 48

Hlubi man riding an ox with plaited bridle. Matatiele, 1961. Photo B. S. Griffin.

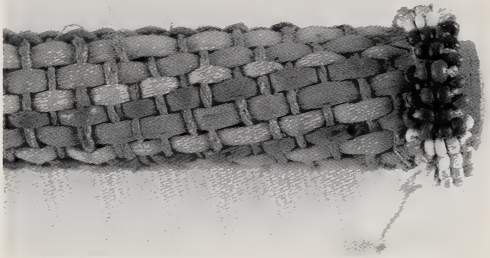


Figure 49

Covering of dancing stick, Xhosa. Total length 981 mm. NCHM ET 1239. Photo NCHM.

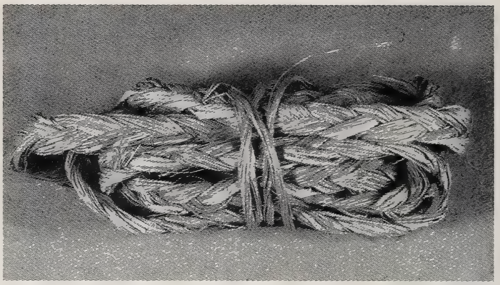


Figure 50

umthwaso, rope, Mpondo, Libode, 1939. SAM–6067.

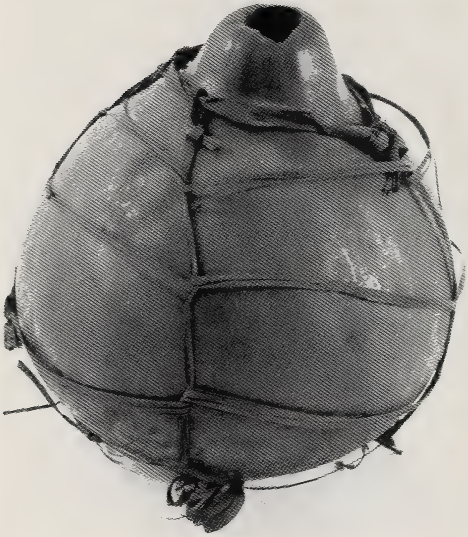


Figure 51

Wrapped sling for calabash (*idliwa*), Mpondo, Lusikisiki, 1935. Diameter of calabash 240 mm. NCHM ET 35/453.

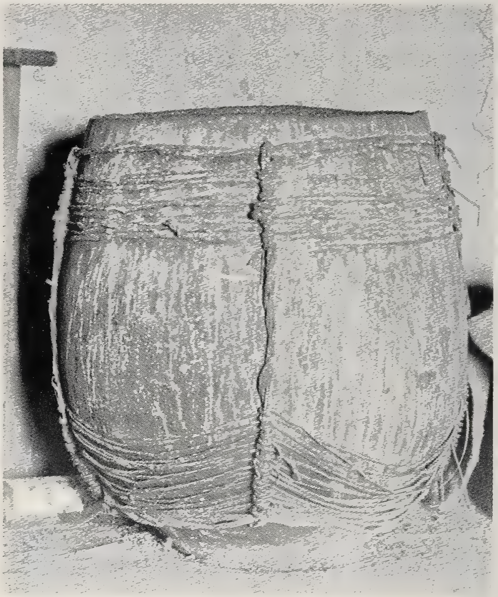


Figure 52

Wrapped strengthening for large pot, Mpondo, Libode.
D & H, 1984.

Records

Early: Nil.

Recent: NCHM ET 1239, Xhosa. Shaw & Van Warmelo 1988: 680, pl. 108 (fig. 2).

Field survey: 1961: Xhosa, Kentani.

5. ***umthwaso***: rope, Xhosa. *intsontelelo*: general. *umbeleso*: Xesibe. An all-purpose rope consisting of a thick three-strand plait of grass, sedge or *Iridaceae* leaves (Fig. 50). Used especially for holding down thatch.

Records

Early: Kay 1827 [1833: 117], Bomvana.

Recent: Shaw & Van Warmelo 1972: 69, 73; 1974: 160, 164, pl. 32 (figs. 3, 4), general. SAM–5626, Mpondomise, Tsolo, 1936. SAM–6067, Mpondo, Libode, 1939.

Field survey: 1955: Mpondo, Flagstaff, SAM–7418. 1961: Hlubi, Matatiele. 1969: Bhaca, Mount Frere; Mpondo, Mevana. 1971: Mfengu, Sotho Location.

6. **Sling**. A sling or framework may be put round a small calabash for travelling. It consists of two or more bound coils of sedge, with sedge warps fastened between them, and sedge wefts wrapped (Fig. 1C) at intervals (Fig. 51).

7. **Support**. A band of wrapped weave is used by Mpondo to support and strengthen large pots (Fig. 52).

Records

Early: Nil.

Recent: Killie Campbell Museum 217. NCHM ET 35/453, Mpondo, Lusikisiki, 1935. Shaw & Van Warmelo 1981: 416, pl. 63 (fig. 6).

Field survey: 1961: Thembu, Hlubi, Herschel. 1984: Mpondo, Libode (D & H).

DISCUSSION

In the range of basketwork of the people of the Eastern Cape, the most notable were the garden and general carrying baskets, the sleeping mats, the food and grain mats, and the beer strainers. In addition, some basketwork techniques were used for ornaments and other small items and in building.

Techniques

Fabric: Writers in the nineteenth century gave the impression, if not the actual statement, that the most important, if not the only, technique used for actual baskets by the Xhosa and the Thembu, with whom they were mainly in contact, was coiled sewn work. It may be presumed that no actual statement to that effect was made because no other technique was seen. A lot of this type of work, especially the particularly fine furcate sewing has disappeared, though some examples survive in museums and a few more recent, rougher examples were seen during the field studies. A heavier coiled sewing is, however, used for garden baskets by Hlubi, some Thembu and some Bhaca, all of whom have long been in contact with South Sotho and who use the term *isiludu/isirudu* which is obviously related to Sotho *seroto*. This somewhat different type of coiled sewing may, therefore, be a borrowing from their neighbours. Mpondo and Xesibe use fine simple sewing over a multiple foundation for palm-leaf beer beakers. Coiled sewing is also used for hats. The Mfengu must have maintained their coiled technique from their former practice in KwaZulu-Natal. No examples of this were seen and it was doubtless overtaken by the techniques taught in school. Weaving techniques are the most commonly seen today.

Lack of documentary evidence makes it difficult to determine all the techniques that were used by people in the east of the area. For garden and general carrying baskets, the technique – among all except the Xhosa, Thembu and Hlubi – was and still is split-warp twine, which in southern Africa is shared only by the Ndebele of Mpumalanga. There is no evidence to show whether or not, in former times, they used other techniques for such baskets.

Plain close twining is used throughout the area for food and grain mats. The Hlubi use twined weave for hats, and the Bhaca used it for penis-sheaths.

Open twined weave is used generally for sleeping mats and other similar mats. Some sleeping mats were seen in which the straight sewn technique had been used. This seems to indicate a vestige of Khoekhoe influence, as Khoekhoe mats were sewn. Open twining is also used for bags, fish bags, and strainers.

Whatever may have been the case in the past, the twined weave has been the most important technique used in the Eastern Cape for some time now.

Twilled weave is used by Mpondo and Xolo for one type of beer strainer and, through influence from KwaZulu-Natal, by the Nzimakwe and others for pouches.

Straight sewing is used for the other type of beer strainer throughout the area.

Wicker- and wattlework in chequer weave have been used mainly in building and fences, as they have been in many parts of southern Africa. But such building techniques are disappearing rapidly from the Eastern Cape.

Plaiting is used for rope and for ornaments.

Beginnings: Roughly the same range of beginnings is used throughout. In flat work, woven or sewn, the elements are laid side by side and joined by the first row of weft or sewing. For ascending woven work, when twined, the warps are bound or looped; when twilled, the elements are knotted in pairs. Ascending coiled sewn work may start with a closed or open ring of foundation, with the sewing or the foundation knotted, or with the foundation bent and sewn over. A method of beginning that is now used for coiled sewn work in palm-leaf, is the chequer square. It has not been established whether this was introduced, nor, if so, where.

Shaping: The common method of increase or decrease in twined or straight-sewn work is to add or take out warps or foundation elements, or to thicken or divide existing multiple warps. Tension is sometimes used. For twilled beer strainers, the natural decreasing width of the material is exploited. In coiled work the placing of the coil regulates the shape.

Shapes: Shapes are practical and dictated by the use for which the object is intended, for example, flanging open from a narrow base to hold a heavy load on the head, or straight sided or slightly narrowed at the mouth to contain liquids. A thin rectangular mat can be rolled up easily and put out of the way when not in use.

Edges: Among the Southern Nguni, coiled sewn work seldom has a special edging, but a change of material for the last round may be used.

The warp edges of flat twined work may be wrapped, scalloped, tucked back, or cut off perhaps after a row or two of close twining. On the weft edges, the weft may be carried straight down to the next row, twined back and forth in a decorative pattern, or wound two or more times round the last warp, which may be thickened.

The circular twined baskets have a scalloped edge, sometimes after a few rows of divided warps. On split-warp twine the edge is often preceded by a band of plain or three-strand twine. Sometimes the last weft is different and stronger.

On beer strainers of both techniques, the beginning knots form the edge, sometimes with the ends left as a fringe.

The warp edge of wicker is stapled.

The edge to the twilled pouch is a selvedge in which the strands are taken back on their tracks. The upper part has its edge finished on the outside and the lower part on the inside, for smoothness in opening or closing.

Finishings: The most common way of finishing is to cut the weaving or sewing strand off with or without a knot, but in sewn work the end of the sewing strand may be oversewn closely. On beer strainers the elements are turned inside and knotted. On bangles the strands are usually bound together, or finished with a spiny cone. Broom handles are seized.

Decoration: The common forms of decoration on twined work are bands of a different twine from the rest of the work, or of a different coloured material, generally horse hair. Geometric designs, sometimes very striking, are made in woven techniques either by the use of a different material or material of a different colour, or, in diaper, by lengthening or altering the stroke. On the twilled pouch of the Nzimakwe a simple pattern is made by using elements of the same material dyed. Very little decoration is recorded on coiled sewn work, but again a design may be made by lengthening the stitch or by the use of a different material, especially horse hair, in the body or for the edge. In the straight sewn cylindrical work of beer strainers, a stripe may be made by altering the ply of some of the foundation strands, or latterly, by introducing colour.

Ornamentation: Ornamental additions, added after completion of the work, are rare and confined mainly to beads and brass buttons on belts and other ornaments.

Utilitarian additions: The few ornamental or utilitarian handles and lids recorded are likely to have been the result of foreign influence.

Tools

Few tools are used.

To cut and trim the material before use and on the finished work: in former times a spear blade must have been the tool used throughout, as there were no knives. Today a knife or a pair of shears is used.

To pierce holes for the sewing strand: an awl, *inyatyhoba*, general; *ilabo*, Hlubi. These have been recorded in wood, iron, iron wire, long thorns or the points of an aloe leaf. For hat-making, the Mpondo use a wooden needle, *isilanda*.

To thread the sewing strand in straight-sewn work: a needle is used today.

To thread the sewing strand through the hole made by the awl in circular work: wooden needles are said to have been used, but in general the sewing strand was pushed through the hole made by the awl. Hlubi said they used two needles, one flat and one bent, or a sailmaker's needle, or the needle might be made from a bucket handle.

To hold the shape of beer strainers: a core of grass was used by Thembu and Mpondo when making straight-sewn beer strainers.

Materials

The most important material for the fabric of baskets, mats and small articles was, and still is, undoubtedly the stem of the sedges, *Cyperus* sp. or *Scirpus* sp. This was used for the weft and often the warp elements of woven work, for the foundation and sometimes the sewing of straight sewn work, and for the sewing and often the foundation of coiled sewn work. Sedge grows especially near the coast and in rivers. It is also cultivated and traded by individuals to areas where it does not grow, and where store-keepers sell it. It is put out in the air to dry and then sorted, and according to the purpose, split and depithed or left whole. Before use it is dampened.

Grass is, however, very important too, especially in the east or in areas away from the coast or rivers, where sedge is scarce and has to be imported. Special grasses are used for special purposes. Grass is plentiful in the autumn and perhaps because of its greater availability, it is often used for the sewing as well as the foundation of coiled work, and for the warps of woven work. It supplies all elements for plain and ornamental plaiting, for which the shiny stemmed varieties were used green, which changed later, with ripeness, to golden yellow. For broom making, the Thembu of Herschel heat the material to split the stems before soaking them.

Rushes are often used instead of sedge for rough mats and bags.

Tail hair and dyed materials are used in decoration.

Materials of less frequent use, but often important, are bark and other plant fibres.

For building techniques, available woods are used, now especially wattle and other *Acacia* species such as Port Jackson, *Acacia saligna* (Labill.) H. L. Wendl.

The following is a list of materials recorded.

GRASSES

ichancasi – grass, for food mats, Thembu, Mpondo

idobo – grass, for making rope, Mfengu, Sotho Location; Mpondo; *ukwame*, Bomvana; for thatching, Xhosa; general term for long coarse grass

incema – grass or short rush (?sedge) for food mats, Thembu, Bhaca, Hlubi; or ornaments, Vundla

incuma – grass for making maternity belts, Xhosa

ingca – general term for grass

injika – grass for bangles, general

inqoqotwane – grass for sewing of *isiludu*, Hlubi

intsimbane – grass, *Setaria sphacelata* Stapf & Hubb., Xhosa

ixonya – grass for making rope, general
ubhijo – grass, *Digitaria* spp. for ornaments, Mpondo, Bhaca
umgwigwi – grass, *Eragrostis curvula* Nees, Mpondo
umhluma – *Hyparrhenia* sp.
umphica – *Digitaria natalensis* Stent, for making ornaments, Thembu
umqungu – grass, *Cymbopogon marginatus* Stapf, for rope, Bomvana
umsingizane – *Sporobolus pyramidalis* P. Beauv., grass used for rope, Bomvana; for garden baskets (*isirudu*), Thembu, Mfengu; for foundation coil of baskets, and hats, Hlubi; for plaited sewing of coiled work, for hats, all except Xhosa; the whole plant is used for coil foundation of grain bins by Hlubi of Herschel
umsuka – tough grass, *Eragrostis plana* Nees, *Hyparrhenia hirta* Stapf, *Sporobolus fimbriatus* Nees, Xhosa, Thembu, Mpondo; grass, *Hyparrhenia hirta*, coil foundation, Thembu, Hlubi, Sigogo; grass, *Miscanthus capensis* (Nees) Anderss., Xhosa, Umtata
umthala – *Miscanthus capensis* Stapf, for rough mats, Xhosa
urasi – grass from mountains for making ropes and brooms, Thembu, Mpondo; *urasi,* grass, for making beer baskets, Mpondo; *irashu*, *Miscanthus capensis* (Nees) Anderss., Xhosa, Umtata; *urasi*, Xesibe, Bhaca; *irasu*, from Umzimvubu River, Mpondo

SEDGES
ikhwane – sedge, *Cyperus latifolius* Poir, for sleeping mats, Xhosa, Bomvana, Mpondo, Mfengu
umzi (pl. *imizi*) – sedge, *Cyperus textilis* Thunb. and other species for baskets, food mats, beer strainers, sleeping mats and maternity belts, general; and for sewing of grain bins, Hlubi. Mpondo plant this variety in gardens or along rivers, where it also grows naturally.
incema – short variety of sedge for food mats, general
ingcema – split sedge for *ingobozi*, Vundla
irwantsi – sedge, *Cyperus sexangularis* Nees, for mats and food mats, Thembu, Mpondo

RUSHES
inkomfe – plant for making rope, Thembu, Bhaca
umcubhatha – rush or sedge, used for tobacco bag and sweating-mat or a baby's mat, Bhaca
utyani – rushes for sleeping mats, Xhosa (Kay 1833: 147)

CREEPERS
umnxeba – wild vine, *Vitis*, general; any fibrous binding material, such as rope, Bomvana, Bhaca
umsonto – rope made of *uluzi*, general
uzunqu – monkey-rope, *Rhoicissus rhomboidea* (E. Mey) Planch., Mpondo; *uzungo*, for wefts of sledges, Mpondo; for oversewing edges of baskets, Xesibe, Bhaca

PLANT LEAVES
ilala – palm-leaf, *Hyphaene coriacea* Kunze (*H. crinita*), Mpondo, Libode and elsewhere; for beer beakers, Mpondo

incaluka – plant of family *Iridaceae*, for ornaments, Mfengu (Kawa 1929)
isundu – palm, *Phoenix reclinata* Jacq., leaves of which are used for *khwetha* skirts, Xhosa; *usundu*, Thembu
ithembu – used for rope, Thembu, Xesibe, probably *Dierama* sp.; leaves of *Hypoxis* sp. for ornaments, Mfengu (Kawa 1929)

BARK

intsontelo – rope made of *uluzi*, general
itwhebu – fine inside bast of tree bark (Kropf 1915)
ixolo – the outer bark of a tree, general
uluzi – inner bark of *Ficus* sp. or any of the other smooth barks, for weft of twined mats and for decoration of baskets; general

FIBRES

uluzi – fibre of *Ficus* sp., used for the sewing or weaving of sleeping mats, general
ikhala – agave, the fibre from its leaves is used for the weft of sleeping mats, Xhosa, Tshabo
ikhamanga – small species of aloe, or ordinary aloe

WITHIES

isiphingo – *Scutia myrtina* Kurz, for wattling cattle enclosures (Kropf 1915)
isithombothi – withies of *Acalypha glabrata* Thunb., for the sides of sledges
ugonothi – wood slivers for making wicker meat tray, Mpondo, Lwandile

ANIMAL MATERIAL

umsundulo – tendons from under the shoulder-blade of an ox, which provide sinew thread, Xhosa
itshoba – ox tail hair, used for decoration, Xhosa, Mpondomise, Mfengu, Hlubi; horse tail hair is also used

DYES

isimoyo – *Acacia* sp., pattern on pouches, Xolo
mtsekisane – *Euclea* sp., pattern on pouches, Xolo

Makers

Women make baskets, mats, some bags, sewn beer strainers, ornaments, brooms and rope. Men make initiation costumes, hats, woven palm-leaf beer strainers, sewn baskets (Hlubi), wicker meat trays and all wicker- and wattlework used in building. There is no record of women doing wicker- or wattlework.

Basketwork used not to be a specialist craft. It has become more so although there was usually, until recently, one person in a family who was able to make actual baskets. Some people make baskets to sell to others or to the stores where others buy their baskets.

Seasons

Although wicker- and wattlework can be done at any time, the late autumn and winter are the main seasons for other basketwork because the material is then ready and, as far as women are concerned, it is the slack season for agricultural work and thus they have time. In the Eastern Cape this means April to August.

CONCLUSION

The people of the Eastern Cape were, by tradition, pastoralists and agriculturalists. For many generations before they settled in the localities now included in the Eastern Cape, they were on the move. It is understandable therefore that light, easily transported equipment, renewable without dependence on, for example, deposits of clay for pottery, should have been important. This seems to have been very marked in the west, where the pottery tradition was weak, and the majority of utensils were of basketwork.

People moving into a new area bring their techniques with them, but it is nevertheless obvious that they must use techniques for which the available material is suitable. This was not much of a problem in this case, because the people came from a floristic region with similar plant species, with the exception of the *Hyphaene* palm which does not occur west of about the Umzimvubu River. One does not, therefore, find regular use of palm-leaf in the basketwork of the west. The *Phoenix* palm-leaves are not strong enough for general use but are used for the young men's initiation costumes.

Inevitably the coverage of this study is uneven in several respects. The early records in the literature refer mainly to the Xhosa and the Thembu, the people of the west, who were the first with whom the early authors were in contact. For the same reason the earliest examples in museums came from the western people, or from the eastern Khoekhoe to whom they were traded. It is not possible, therefore, at this stage, to be precise about what were the former differences in basketwork techniques between the respective Southern Nguni groups. Proximity has brought about near uniformity in this respect.

These aspects are reflected in the range of sources and museum specimens quoted, as is the fact that, as the years passed, authors and collectors of basketwork were active further east and the western people were exposed to alternative materials and articles and became less and less dependent on basketwork. In the fieldwork, it was attempted to cover the whole area, and it became evident that, at the time that the study was undertaken, the pattern was the same in that the eastern people still had great reliance on basketwork, while those in the west used the technique less.

The following are the differences in technique, and the range of objects used, that appear to have been characteristic of different people or in different areas.

1. *Fine, furcate, coiled sewn work* of Xhosa and Thembu, apparently used formerly by them for all baskets, but now disappeared. It seems to indicate a different tradition from the twined woven work of the others. It has not been recorded elsewhere in southern Africa except on the edges of the main area, that is, in Lesotho, northwestern

KwaZulu-Natal and Bomvanaland. Xhosa and Thembu milk vessels were made in this technique, whereas other people of the Eastern Cape used pottery or wooden milk vessels.

2. *Split-warp twined weave* used by Mpondo, Bomvana, Xesibe, Mpondomise and Bhaca, for all baskets. This technique was also used by the Ndebele of Mpumalanga for basketwork lids for pots, but was not seen elsewhere in southern Africa.

3. *Straight sewn* technique for furnishing mats, recorded from the west, presumably reflects former Khoekhoe influence, since in both west and east of the area, the twined technique is generally used for such mats.

4. *Twilled palm-leaf weave* used for beer strainers and pouches by the Mpondo, Xesibe, Xolo and Nzimakwe, all living in the area of the *Hyphaene* palm, and having historical connections with the KwaZulu-Natal region and proximity to the east African basketry. It is, in fact, used further inland, wherever the palm or a suitable flat leaf is available.

5. *Fine simple oversewing on a coiled foundation*, with strands of palm-leaf, of the Mpondo and Xesibe beer beakers. This technique again seems related to KwaZulu-Natal and, of course, to the area of the *Hyphaene* palm. In other areas pottery is used for drinking beer.

6. *Plain coiled* basketwork of Thembu and Hlubi seems to show definite South Sotho influence, but it is, however, widely used.

7. *Thickly coiled sewn* grain bins in use in the northeast of the area instead of storage pits as in the west.

8. *Straight sewn* beer strainers and *twined* food mats are characteristic of all Nguni-speakers, but are also known among other peoples in southern Africa.

9. *Woven* penis-sheath, used by the Bhaca.

It is worth noting that, of the three predominant techniques used for actual baskets, one – coiled, with simple oversewing – is common all over Africa and elsewhere in the world; another – coiled, with fine furcate sewing and now obsolete among the Southern Nguni – has been seen in recent times in rougher form, only in Bomvanaland and at the southern border of Lesotho and the northwest corner of KwaZulu-Natal but not elsewhere in southern Africa; and the third – split-warp twined weave – used in the east of the area, was also used for one article among the Ndebele of Mpumalanga, but there is no other record of it in southern Africa. The significance of these differences has not yet been established.

During the last 200 years, much soft or domestic basketwork has been taught in the schools. For the most part the technique has been a quicker, looser and less-durable coiled sewing. Undoubtedly, a lot of these baskets were made for use, especially in the early days, but in addition a lot were made for sale locally. From the early 1800s, there was regular trade, and it is recorded that Xhosa brought baskets and mats to trade at the Fort Willshire Fair. Baskets are still used by the Southern Nguni themselves, and some are made for sale, but there has not been the large development of production for export, such as has flourished in KwaZulu-Natal (Vukani) and Botswana (Botswanacraft).

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ABBREVIATIONS

AM	MuseumAfrica, Johannesburg (formerly Africana Museum)
Cambridge	Cambridge University Museum of Archaeology and Ethnology
Copenhagen	National Museum, Copenhagen
D & H	Patricia Davison & Lindsay Hooper, Iziko Museums of Cape Town, fieldwork 1984–1986
EL	East London Museum
FH	F. S. Malan Museum, Fort Hare
Liverpool	Liverpool Museum
MM	McGregor Museum, Kimberley
NCHM	National Cultural History Museum, Pretoria
PR	Pitt Rivers Museum, Oxford
pers. comm.	personal communication
SAM	South African Museum, now incorporated in Iziko Museums of Cape Town
Stockholm	Statens Etnografiska Museum, Stockholm
TM	Transvaal Museum, ethnographic collection, now in National Cultural History Museum, Pretoria
UCT	University of Cape Town collection, on permanent loan to Iziko Museums of Cape Town
US	University of Stellenbosch

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THE FABRICATION TECHNOLOGY OF SOUTHERN AFRICAN ARCHAEOLOGICAL GOLD

by

DUNCAN MILLER

&

NIRDEV DESAI

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THE FABRICATION TECHNOLOGY OF SOUTHERN AFRICAN ARCHAEOLOGICAL GOLD

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ABSTRACT

Gold has been produced in southern Africa for nearly 1000 years. This paper records the study of gold assemblages from the South African sites of Mapungubwe and Thulamela, and from sites in modern Zimbabwe. The gold fabrication technology was indigenous, and derived from that employed in copper working. Sub-spherical gold prills, probably formed by pouring molten gold into water, were punched using a four-sided tapered punch to make solid gold beads without a join. Some of these were decorated by regularly spaced indentations in the outer margins. Other beads were made from wrapped strip or short lengths of wire, which was hammered rather than drawn. Hammered gold sheet was attached to presumably wooden forms using square section tacks cut from tapered rod and hammered in cold, forming a flattened head. The sheets and tack heads were scratch burnished to create a sheen on the exposed surfaces. Gold sheet was also cut into narrow strips for helical wound bangles, which were also made from hammered wire. There was no evidence of soldering or heat treatment other than annealing.

Ann. S. Afr. Mus. **111** (2), 2004: 79–102, 12 figs, 2 tables.

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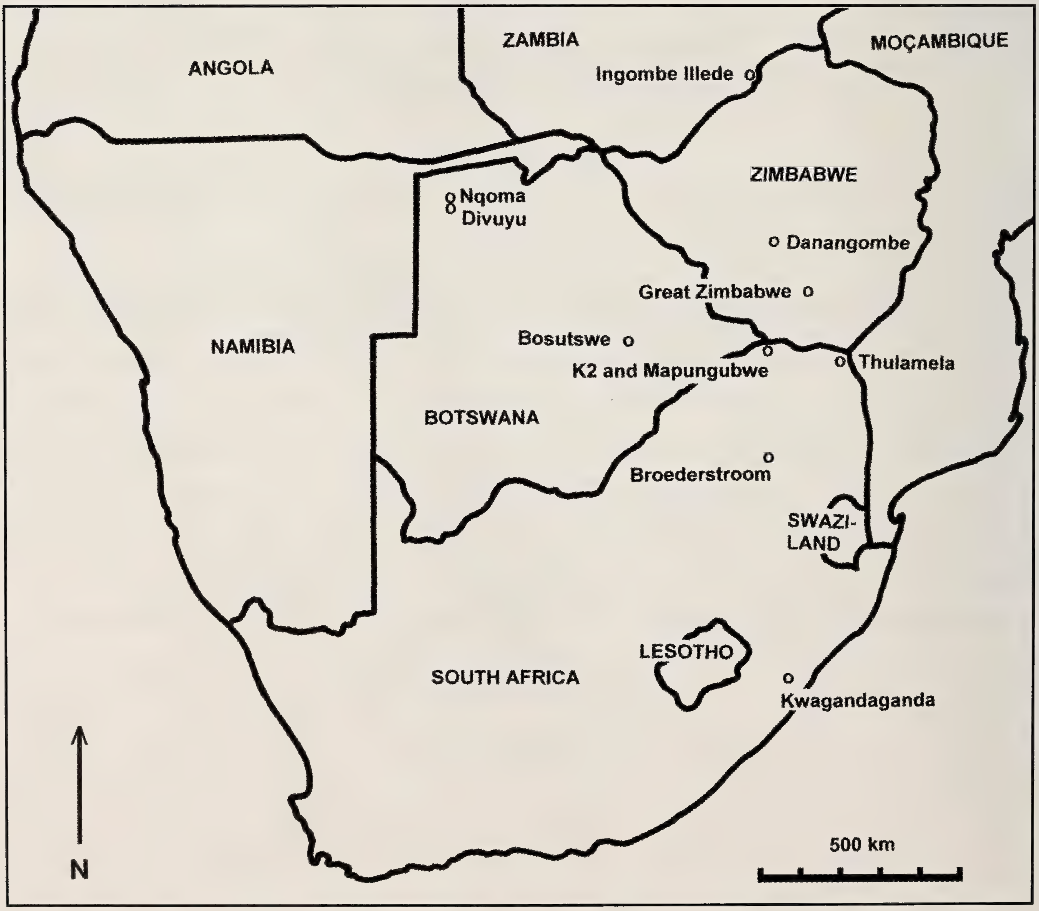

Figure 1
Map of southern Africa, showing the archaeological sites mentioned in the text.

INTRODUCTION

The clearest evidence for the early use of gold in southern Africa is in the form of gold mines on the Zimbabwe plateau, with dates that span the last 1000 years (Summers 1969; Swan 1994). Gold mining was stimulated by increased trade with the East Coast, that started in the late 1st millennium AD (Phimister 1976; Miller *et al.* 2000). This trade contributed to significant economic changes that in turn led to the rise of a complex social structure, with an elite living in walled hill-top sites like Mapungubwe, Great Zimbabwe and Thulamela (Huffman 1996). The East Coast trade was usurped by the Portuguese at the beginning of the 16th century AD, but it never flourished to the same extent as the earlier Islamic trade, and gold production declined sharply. Various lines of evidence allow us to describe the history of indigenous gold mining and the gold trade (Miller *et al.* 2000), but there are technical questions pertaining to the production and fabrication technology of jewellery manufacture which have not been answered satisfactorily. This paper reports the visual inspection and metallographic study of a representative sample of southern African archaeological gold artefacts, in order to describe the techniques used in their manufacture.

PREVIOUS STUDIES

Previous studies of southern African gold artefacts have not reached a consensus on the fabrication technology employed. The early studies were either very superficial, or consisted in making interpretations based on very small sample sizes. Fouché (1937) reported studies of a small sample of gold artefacts from Mapungubwe (see Fig. 1) conducted by a number of metallurgists. Weber studied eight beads from this site and together with Pearson noted that the beads had punched holes (Fouché 1937). Nevertheless, Pearson also suggested that these beads may have been cast with holes in place (Fouché 1937; Meyer 1998). Stanley observed that the Mapungubwe gold beads were of punched and wrapped varieties, and that cold and hot working as well as casting were used in the fabrication process (Fouché 1937). Beck attempted to measure the density of the gold as a test for purity, but submersion in water for hydrostatic weighing was unsuccessful due to gas bubbles sticking to the beads (Fouché 1937). Beck also studied some samples microscopically for methods of manufacture, which revealed that individual beads were either wrapped or cast. The gold foil sheets were made by hammering on a flat surface and were cut into sections with a sharp-edged object. It appeared that the holes for nails were punched in, and not drilled. It was speculated that some beads may have been drawn wire bent around, or wire was flattened and then punched through the centre when cold (Fouché 1937).

The gold work from Mapungubwe, Great Zimbabwe, Ingombe Ilede and Dhlo Dhlo (Danangombe) was described in much greater detail by Oddy (1983, 1984). Oddy concluded that the fabrication technology was relatively unsophisticated, and that there was no evidence to suggest that it was not indigenous, particularly because of the absence of soldering. Hammered foil was attached to wooden forms by creasing and folding, and tacked into place with gold pins (Oddy 1984: 72). Three types of beads were identified from Mapungubwe: cast flattened spheres with the holes apparently 'cast-in'; similar beads with grooved margins; and beads of wrapped 'wire' made by hammering. Some of the wire from Great Zimbabwe showed signs of wire drawing, and wire drawing implements (and other blacksmiths' tools) were recovered from Ingombe Ilede. Nevertheless, gold wire from this latter site appeared to have been hammered rather than drawn. In other respects there was no significant difference between the gold from the various Iron Age assemblages. Meyer (1998) reiterated Oddy's interpretations for the gold from Mapungubwe.

THE MATERIAL STUDIED

Gold assemblages studied here came from Mapungubwe and Thulamela in South Africa, and from historic collections made in Zimbabwe (Fig. 1). The Mapungubwe cluster of sites dates from the early 11th to early 14th centuries AD, but the important Mapungubwe gold burials date to the mid to late 13th century AD (Vogel 1998; Meyer 1998). Most of the gold from Mapungubwe was poorly provenanced, but by far the majority originated from the burials on the Hill (Fouché 1937; Miller 2001). Much of the Zimbabwean material is thought to have come from Great Zimbabwe (Desai 2001), but some of it may have originated from other Zimbabwe culture sites looted in the late 19th century AD (Swan 1994; Miller 2002). Consequently, the material from Zimbabwe may span the period from the 14th to mid-19th centuries AD (Huffman 1996). Thulamela has radiocarbon dates ranging from the 14th to 17th centuries AD (Küsel 1992; Steyn *et al.* 1998). Most of the gold from Thulamela was collected in 1996 from the two elite burials excavated by the team led by Sidney Miller (Steyn *et al.* 1998) and from the earlier midden excavations (Küsel 1992).

Two sets of samples from Mapungubwe were analysed metallographically to characterise the fabrication technology in detail (Table 1—see page 96). The first set, M1231 A–Q consisted of representative material selected by Professor Andrie Meyer of the University of Pretoria from their collections for analysis. There were seven beads, one gold globule, four pieces of gold helices, two tacks, one wire, one foil sheet and one strip. Two additional beads from the University of Pretoria collections, M870 and M1118 were studied visually without analysis. The second set analysed, UCT A–L, was a small collection of Mapungubwe gold work in the collections of the University of Cape Town (UCT). This group consisted of four tacks, one helix, one sheet, and beads divided into four subgroups (on the basis of their size and mode of manufacture) containing six beads, three beads, fifteen beads, and seven beads respectively. In all, twenty seven gold artefacts were analysed metallographically. All these samples were tested at UCT for major element content by energy dispersive X-ray (EDS) fluorescence in a fully analytical Leo S440 scanning electron microscope, using freshly ground and polished sections through the bulk of each artefact to avoid surface enrichment or contamination effects. This system has a detection limit of about 0.1% for metals such as copper and silver which could be expected as possible alloying elements.

The larger collections of Zimbabwe and Thulamela material were studied visually with the intention of determining any possible significant differences from the earlier Mapungubwe material studied metallurgically (Desai 2001) and material illustrated in publication (Fouché 1937; Meyer 1998). The substantial collection of gold thought to originate from Great Zimbabwe, donated by Cecil John Rhodes in 1874, is housed at the South African Museum in Cape Town. These artefacts are glued onto a flat opaque surface for exhibition purposes and could be viewed from one side only. A total of sixteen pieces of foil, one hundred and forty six tacks, sixty four beads, twenty one pieces of assorted wire, seven links, five nuggets and nine spherical cast droplets or prills from this collection were inspected (Desai 2001). Another collection of Zimbabwean gold, also thought to originate from Great Zimbabwe but possibly including material from later Zimbabwe culture sites, is in the Rhodes collection at his former home, Groote Schuur in Cape Town. These pieces had no detailed provenance. They were not described in terms of their fabrication technology, but were sampled with material from the other collections for trace element analysis, reported elsewhere (Grigorova *et al.*1998; Miller *et al.* 2001).

METALLOGRAPHY AND RECONSTRUCTION OF FABRICATION TECHNOLOGY

The detailed descriptions of the artefacts studied visually are recorded in Desai (2001) and the results of the metallographic analyses are summarised in Table 1. Metallography was performed only on gold samples from Mapungubwe, in order to confirm the reconstruction of the fabrication technology suggested by the visual inspection.

The metallographic study revealed the following common characteristics. There was very little corrosion in any of the gold artefacts. Silver was the only detectable major element other than gold, ranging from 2% to 12% Ag. This matches the range of silver occurring naturally in material from the Witwatersrand gold fields (Erasmus *et al.* 1987). The silver content did not correlate with artefact type, and does not indicate intentional alloying. The metal was homogeneous, and there were no inclusions. All the finished artefacts were both cold worked and annealed at some stage of manufacturing. There was no evidence of welding or soldering.

The gold artefacts from all the assemblages studied could be described in terms of seven categories, based on their morphology. These were foil, tacks, prills, beads, rod sections, wire, and discs.

Gold foil, or sheet ranging from 0.3 to 0.5 mm thick, was well represented in all the collections. Original size could be estimated if the foil contained punch marks, since these marks would have been on the edges of the foil pieces (Fig. 2). Most individual pieces were usually no larger than 20 mm by 30 mm, although the gold rhinoceros from Mapungubwe (Meyer 1998) was made from substantially larger sheets. The punch marks themselves were usually square, reflecting the square cross section of the tacks (Fig. 3). All the sheets were pitted and rough on one side, evidently from being hammered out on a granular stone anvil. Sheets were cut to the required size by using either a chisel or a blade, or simply used as is with the ragged edges hidden by overlaps, pinned in place on wooden

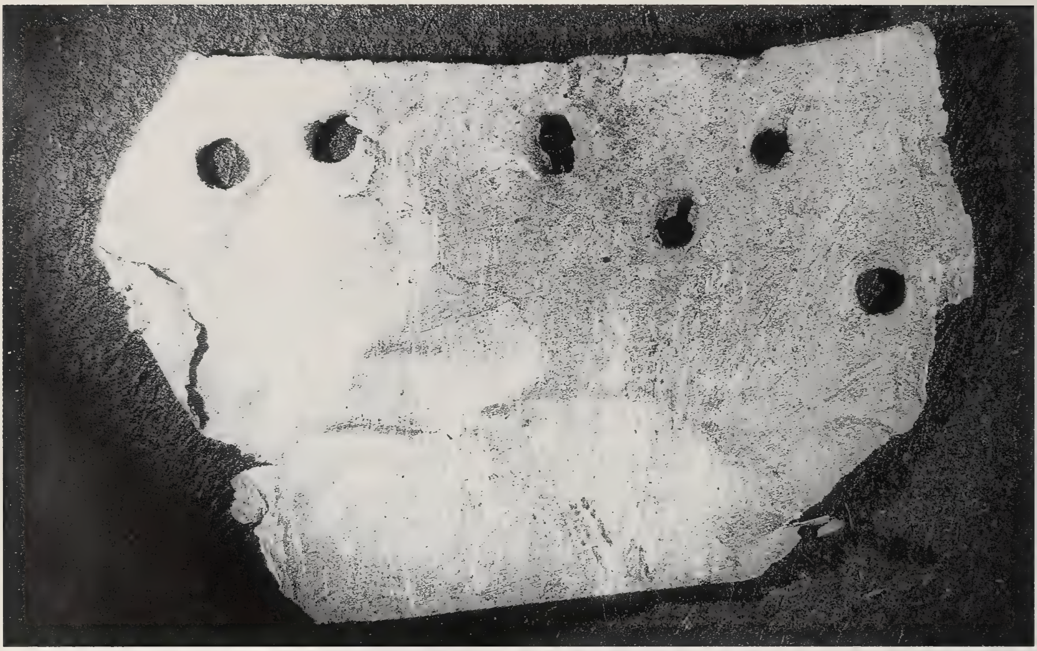

Figure 2
A perforated gold sheet from Mapungubwe, showing the scratch burnish on the outer surface (magnification 4×).

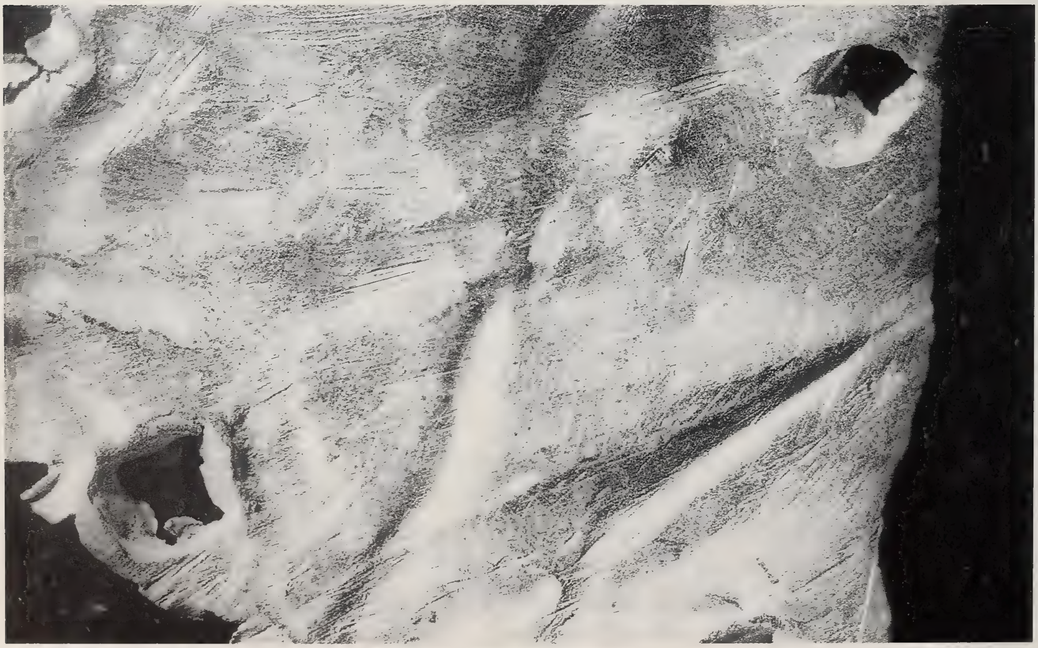

Figure 3
A perforated gold sheet from Zimbabwe (SAM 7904), showing square tack holes and a ragged edge (magnification 6×).

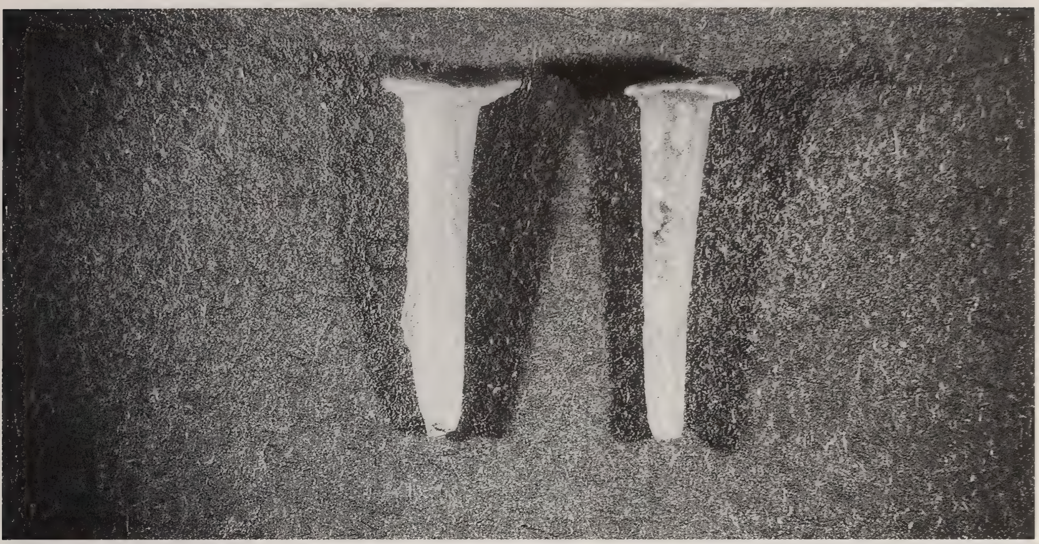

Figure 4
Two gold tacks from Mapungubwe, showing heads formed in use (magnification 4×).

forms with gold tacks. Finally, the exposed surface was scratch burnished, resulting in a shine. As overlapped areas of foil were not scratch burnished one can deduce that the foil was burnished after it was attached to the object to be covered. Two fragments of sheet were analysed metallographically. The grains were recrystallised, equi-axed and angular. The grain sizes varied considerably, from a coarse ASTM 4 to a fine ASTM 8.

The tacks were four-sided, tapering, wedge-shaped pieces of gold that were between 3 mm and 10 mm long (Fig. 4). The tacks were made by hammering the end of a piece of wire into a four-sided point, and then cutting off the short tapered section, presumably with a chisel. The flattening of the heads took place by hammering the tacks into the substrate, as evidenced by the metallographic study of three of the tacks. The grains of used tacks were heavily deformed, particularly in the flared heads (Fig. 5). The grain sizes of these tacks were generally quite small, ranging from ASTM 6 to 8. The tack with the largest grains, UCT D, had a grain size of ASTM 5. It was also not as deformed along its length as the others, lacked a head, and was probably an unused tack blank.

Prills, or cast droplets, were spherical pieces of gold found in diameters from 0.5 mm to 12 mm. They were used to make various items such as punched beads, or flattened into strips or foil. The casting of these small droplets accounts for the voids or ‘air bubbles’ noted by Oddy (1984:73). Larger prills or nodules may have been buttons of gold recovered from melting crucibles. The smaller spherical droplets were probably formed by pouring molten gold into water, or melting filings or short pieces of wire in a crucible packed with charcoal. Pearson suggested that prills could have been formed by spilling the molten gold onto a flat surface, with the molten gold forming globules as it cooled (Fouché 1937). This untested method appears unlikely given the ease of producing gold shot by pouring molten gold into water.

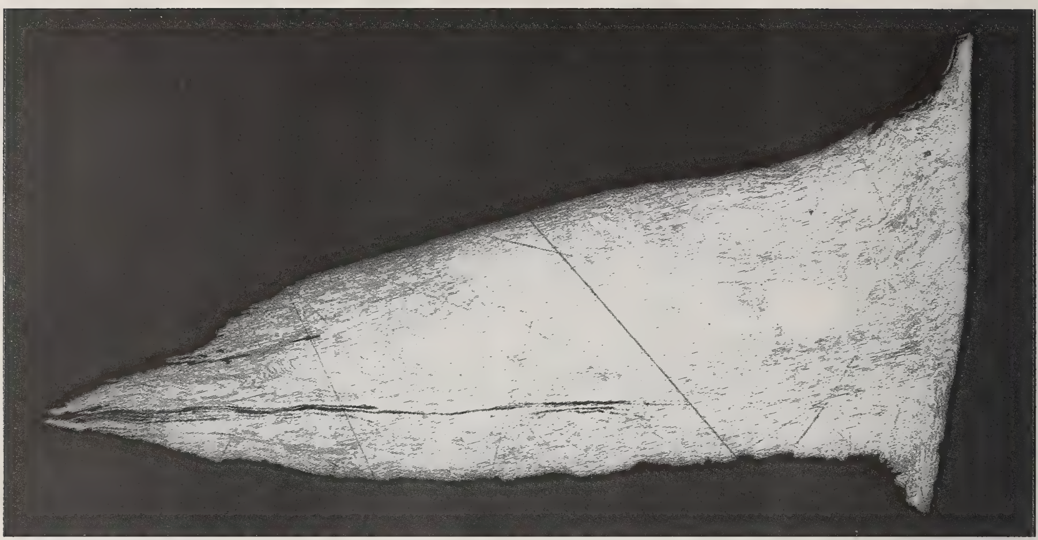

Figure 5
Etched section through a gold tack from Mapungubwe, showing longitudinal cracks running down the length of the shaft and intense cold work deformation in the head (magnification 18×).

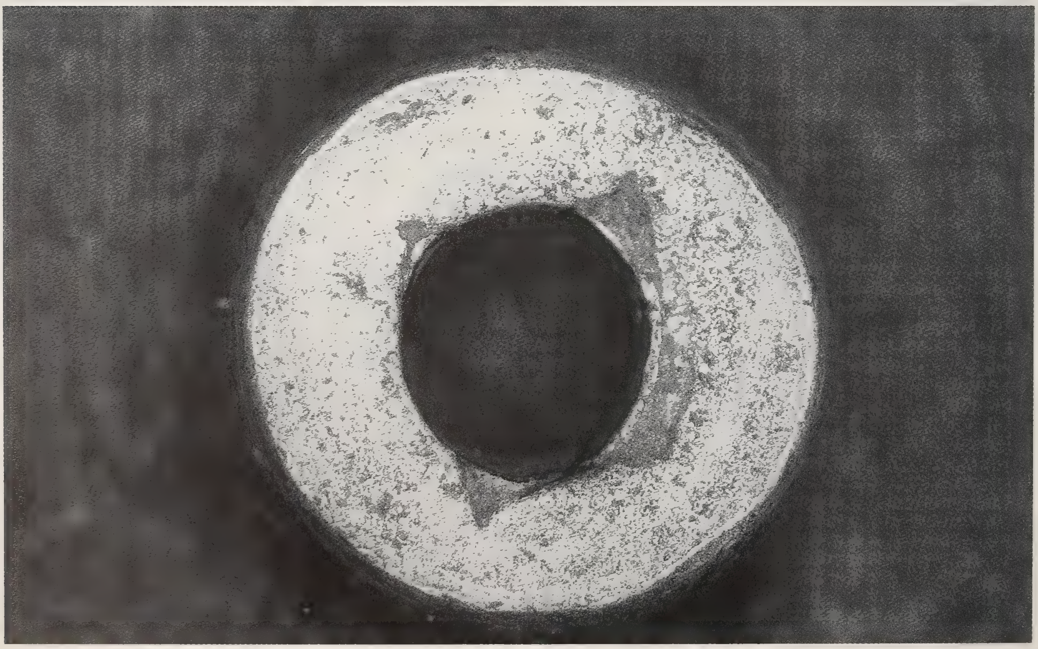

Figure 6
Punched solid gold bead from Mapungubwe, showing four indentations from the sharp edges of a tapered, square-sided punch (magnification 12×).

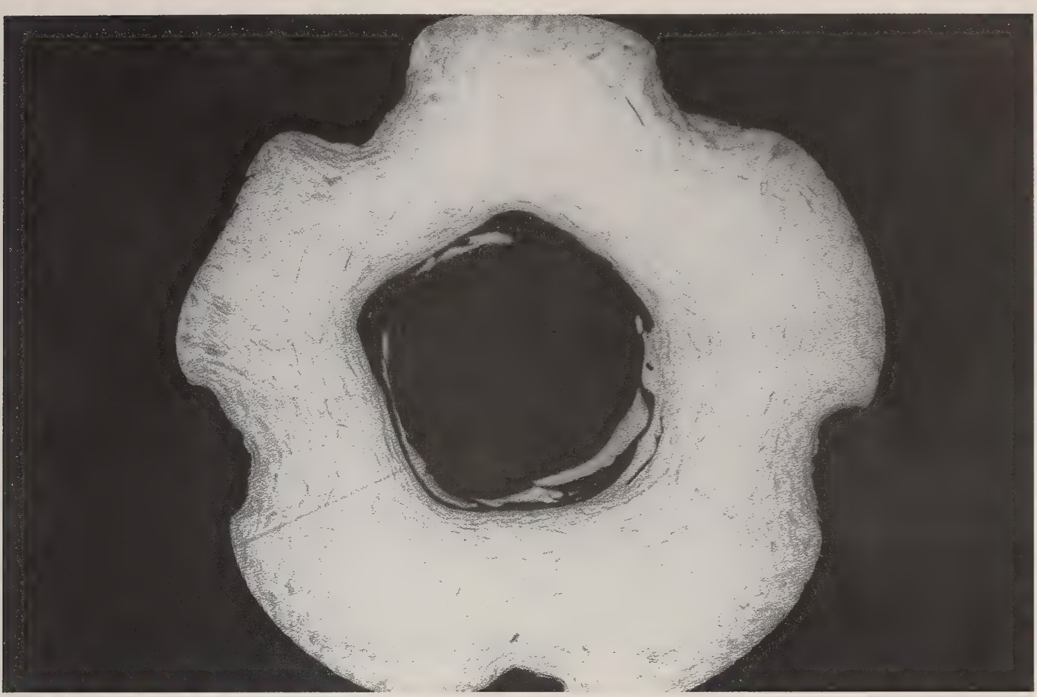

Figure 7
Grooved solid gold bead from Mapungubwe, showing five indentations impressed into the outer margin (magnification 14×).

Bead sizes ranged between approximately 2 mm and 5 mm in external diameter, with an internal diameter ranging from 1 mm to 3 mm. Most of the gold beads analysed and described in the current study could be categorised into two groups distinguished by the means of manufacture; punched or wrapped. Punched beads were sub-spherical items with single holes and no visible join. The grain sizes varied from relatively large (ASTM 4) to very fine (ASTM 10), indicating different degrees of cold work before the final anneal. They were indeed punched, and not cast with holes as proposed by Oddy (1984) and earlier investigators (Fouché 1937). There were traces of four evenly spaced indentations on the edge of the internal diameters on both the flattened end surfaces of most of these beads (Fig. 6), although in some specimens these indentations had all but disappeared through wear.

After somewhat flattening spherical prills or shot on an anvil, beads were punched from both sides with a square punch that left a four-sided squarish hole, sometimes with cracks extending from the sharp corners. Stringing wear subsequently rounded the aperture. Only one exception to the punched square hole was noted, where a circular round bead had a round indentation punched from one side only. A possible explanation for the preference for a square punch is that it remained sharper for longer and was easier to sharpen with four hammer blows at the tapered edge. The punch used for making holes in the punched beads was probably made with an iron tip, as it was the hardest metal mined in the southern African Iron Age and could easily pierce through a small gold prill.

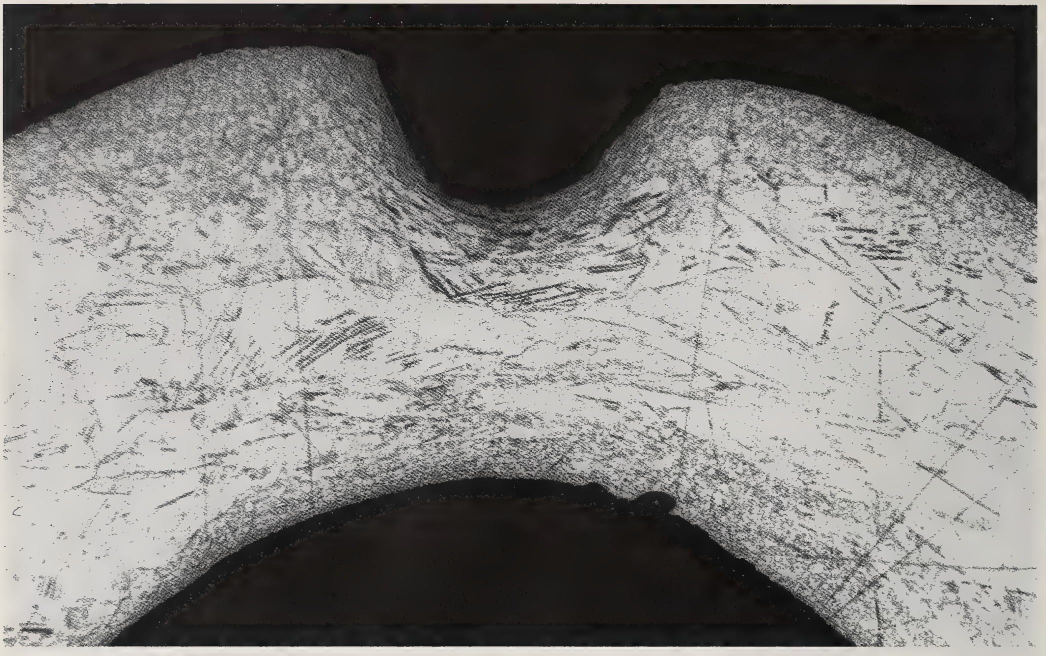

Figure 8
Etched section of grooved gold bead from Mapungubwe, showing the intense cold work at the base of the groove which was indented cold (magnification 56×).

Figure 9
Wrapped gold bead from Mapungubwe, showing an open join (magnification 12×).

Intensely cold worked copper is also a possibility but is less likely, since iron was available and the iron point would last longer.

Some beads had five decorative indentations equi-distantly impressed on their outer circumferences. This grooving, presumably with a light tap by a carefully orientated chisel, produced visible cold work deformation beneath the indentations and often deformed the pre-existing hole into a pentagonal shape (Fig. 7). Oddy (1984) had been unsure if these grooves were cast in place or cut. The grain deformation visible in the metallographic sections proved that these grooves had been indented after punching the central hole, and while the bead was cold (Fig. 8).

There were also large numbers of wrapped gold beads. These were round, often with flattened end surfaces, and to the naked eye looked superficially similar to punched beads, but the wrapped beads were often cruder and less symmetrical (Fig. 9). The most obvious difference between wrapped and punched beads was the presence of a join in the former, usually visible with the naked eye. In metallographic section, most of the beads had extensive cold work deformation in the grains adjacent to the join, showing that they had been hammered closed while cold. There was an equal number of wrapped beads with annealed and recrystallised grains compared to those with deformed grains present throughout the material. This indicated that a final anneal was not standard practice. In the annealed examples, the grain size ranged widely, indicating different degrees of prior cold work. As with the punched beads, residual cold work deformation on the outer margins was due mostly to use wear.

To make a wrapped bead, a strip was cut from roughly square gold wire, and then bent around a thick iron wire used as a former. Often the wrapped beads were barrel shaped and not flattened at the ends as much as the punched beads. Incompletely closed beads were produced that could be squeezed closed by hammering around the join, which often showed cold work. Another type of gold bead was found at Mapungubwe, best described as rolled beads, and illustrated in Meyer (1998: 248). Gold foil was used to make a tapering tongue-like strip, which was wrapped around a wire former several times until the strip was completely wound into a tube, and the former withdrawn.

A representative set of beads and one unperforated prill were sampled for microhardness testing (Vicker's microhardness, 10g load, 10 second dwell time) (Table 1). The purpose of this exercise was to show whether or not a relationship existed between a bead's being punched, wrapped, annealed or finally cold worked, and the microhardness of the metal. There was a positive relationship between the final working stage and the microhardness of the metal, with annealed pieces being the softest and cold worked pieces being the hardest, as expected. The worked beads (mean Hv 62) were two to three times harder than the unworked cast prill tested (Hv 21). In addition, from the metallographic analysis it was clear that annealing was not practised systematically and in some cases a final, possibly accidental anneal, had overprinted earlier cold work deformation.

Links were like wrapped beads, bent around a flattened or rounded wire, without the join being closed. In many cases they were probably simply wrapped beads that had been pulled open during use. Alternatively they could have been an intermediate stage for making wrapped beads, or used as ornamented clips, such as the ones found on the

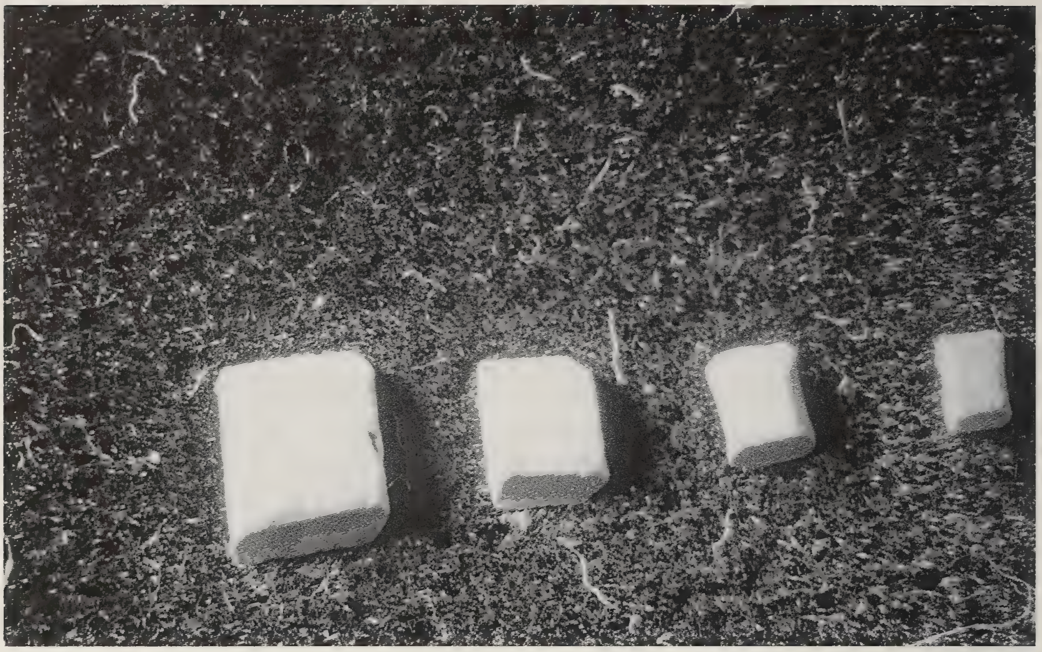

Figure 10
Offcuts, or small pieces of square gold wire from Zimbabwe (SAM 7903), showing chisel cut ends (magnification 4×).

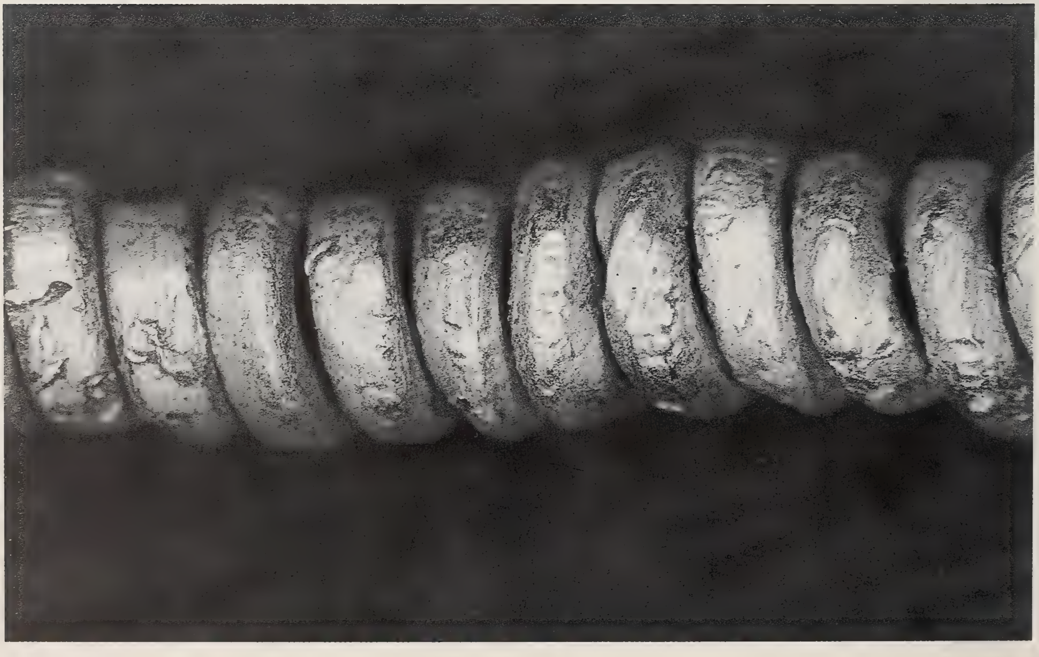

Figure 11
Gold wire helix from Mapungubwe, showing irregularity of the wire and flattening of the outer margins through wear (magnification 10×).

corroded iron necklace of the male burial at Thulamela (Miller 2002). No gold chains occurred in any of the assemblages studied.

Rod sections, or offcuts, were generally square-shaped in cross-section, made by cutting a rod or fine bar into various lengths with chisel cuts, at an angle between 60° and the perpendicular (Fig. 10). The South African Museum catalogue recorded these pieces as ‘weights’, but there did not seem to be a standard size or range of masses for these pieces. The most plausible interpretation is that these rod sections were intended to be flattened to make foil or to be hammered out to form wire for helices.

Earlier studies found evidence for production of Late Iron Age southern African gold wire by drawing it through successively smaller holes in a perforated draw plate. Fouchè (1937) and his colleagues suggested that the wire from Mapungubwe was drawn in this way, as opposed to being beaten into shape. Oddy (1983, 1984) noted that Mapungubwe gold wire did not appear to have been drawn, although there was evidence for gold wire drawing from Great Zimbabwe, with both drawn and beaten wire, including wire with a D-shaped cross section. Gold wire from Ingombe Ilede did not appear to have been drawn, although wire drawing dies were found at this site (Oddy 1984). According to Swan (1994: 67), there is evidence in the form of draw plates from Great Zimbabwe and other Zimbabwe sites that gold wire was made by drawing. In the current study, only beaten wire was identified in all three assemblages. There was no evidence of the consistent longitudinal striations associated with wire drawing, but rather a faceted, scaly appearance on the unworn inner surfaces of the wire coils. It appears that all the gold wire inspected in this study was made by hammering, and that the D-shaped cross sections were the result of wear or deliberate flattening of the outer surface of originally round wire (Fig. 11). The discrepancy with earlier studies may be due to the small size of the collection from Zimbabwe available for this study. The issue of gold wire drawing needs further investigation through the metallographic analysis of well provenanced material in the national collections of Zimbabwe.

Coiled wire helices were made by hammering a length of wire to the desired thickness, accompanied by turning to round and stretch the wire. Then the gold wire was wound around a flexible fibre core to form a helix (Meyer 1998: 247). The wire itself could have been round or squarish, similar to that used to produce the links and the wrapped beads. M1231 P and M1231 Q were the only two pieces in this category studied metallographically. In cross section they were flattened on the outside through wear, and some cold work deformation was present on the outer margins. Strips of flat ‘wire’ were cut from gold sheet with a blade and wrapped around a core to form a helix. Individual windings had characteristic trapezoidal cross sections (Fig. 12). Invariably they had been wound with the two cut edges on the inside of the helix, to provide a smooth outer surface. Short helices may have been used as beads. The longer ones were made into bangles or necklaces, sometimes combining more than one wound strand in a plaited arrangement, as in the bangle from the female burial at Thulamela.

Discs were flattened prills made by hammering flat a large nodule. Many of them had cracked edges (Meyer 1998:251, 252), and their use is unknown, but they were probably precursors to making sheet.

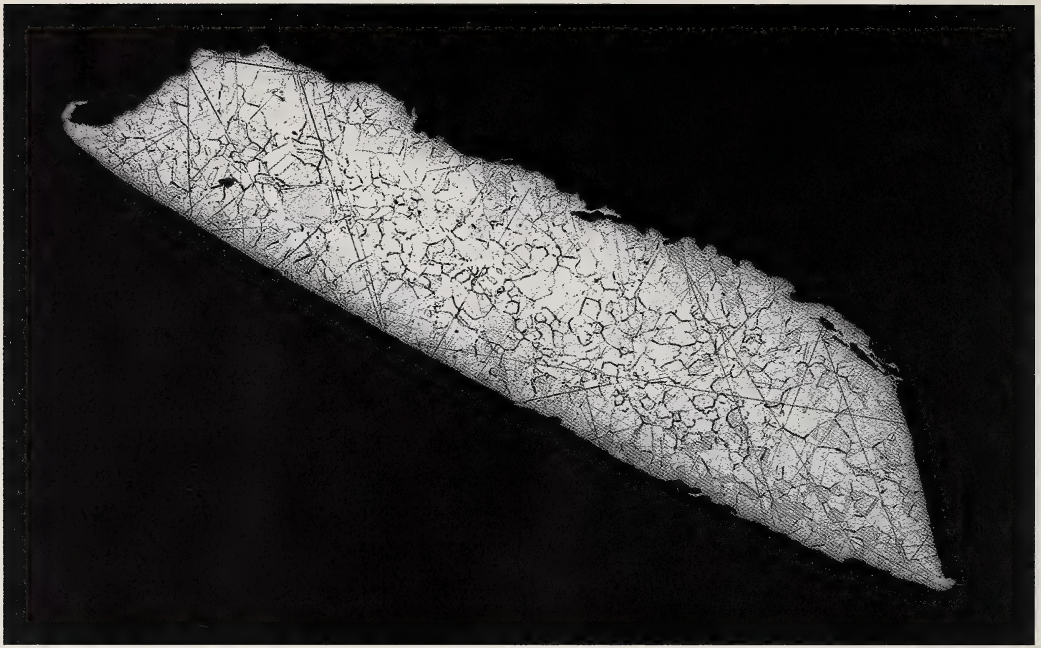

Figure 12
Etched cross-section through one segment of a helically wound gold strip from Mapungubwe, showing residual burrs at each end from cutting with a chisel or a knife, and angular annealed grains (56×).

Secondary ornamentation was limited to indenting, as in the pentagonally grooved gold beads. From Mapungubwe there were small sheets with raised areas, some of them indented with a round indentor from the inside to produce rows of knobs on the outside (Oddy 1984). There were also raised sheets decorated with linear indentations arranged like hatch marks on the outside (Meyer 1998). The Mapungubwe gold rhinoceros was scored similarly to indicate hair on its rump.

It was clear that the basic fabrication technology of the gold artefact types produced was the same for all three assemblages, and that a standardised means of fabrication was used to produce each of the four main different types of finished artefacts – beads, wire, sheet, and tacks. The tool kits used to produce these artefacts have not been found in association with metal working areas on these sites. Nevertheless, all of these gold artefacts could have been produced with a tool kit consisting of bellows, melting crucibles, working surfaces like stone anvils, stone or iron hammers, straight iron wire, a sharp four-sided punch, a blunt round-ended punch, various chisels, and sharp cutting implements like knife blades. The skill in working in producing thin sheet, fine wire, and tiny beads was evident, despite the simplicity of the technology.

COMPARISON WITH OTHER METAL ASSEMBLAGES

Metallographic analyses have been performed on a number of ferrous and non-ferrous metal assemblages from southern African Iron Age sites, reported in Miller (2002). These sites are Broederstroom (Mason 1981; Huffman 1993), Divuyu (Miller 1996), Nqoma (Miller 1996), KwaGandaganda (Miller & Whitelaw 1994), K2 and Mapungubwe (Meyer 1998; Miller 2001), Bosutswe (Plug 1996; Denbow 1999), Great Zimbabwe (Huffman & Vogel 1991), and Thulamela (Steyn *et al.* 1998). Together the metallographic analyses provide a comparative basis against which to assess the gold assemblages reported here.

Table 2 (see page 102) illustrates the occurrence of jewellery items made in different metals from these major southern African Iron Age sites. Gold working was preceded by copper and iron working in southern Africa. Bronze and brass (more strictly a ternary alloy known as gun-metal) first appeared in the archaeological record in the later part of occupation at Mapungubwe, simultaneously with the appearance of gold (Miller 2001). The assemblages from Bosutswe, Great Zimbabwe and Thulamela also contained numerous bronze pieces (Miller 2002) in addition to gold. Both gold and bronze appear to have been used only for jewellery or elite insignia, and were valued locally for their aesthetic appearance.

The fabrication technology employed in working copper, bronze and gold was very similar, with slight variations which exploited the superior malleability of gold. Copper alloys and gold were hot worked to shape with no evidence for soldering. Most of the copper artefacts were generally left in the annealed state, but the gold microstructures were often deformed by subsequent cold work, often unintentionally through use wear. Metal smithing generally seems to have involved cycles of hot and cold work, with no other systematic heat treatment (Miller 2002).

The only evident differences between the metal working processes of gold compared to the other metals in southern Africa were in the few artefact types that were made only in gold, such as tacks and punched and rolled beads, which exploited the intrinsic malleability of this metal. The advent of gold led to some innovation in design and technology, first using gold sheet to ornament wooden forms at Mapungubwe (Miller 2001). This style of ornamentation was present in both the Zimbabwe and Thulamela assemblages, and in the latter case ornamental sheets held in place with tacks were produced in bronze as well (Miller 2002). In only this instance, the novel fabrication technology which made its first appearance with gold was transferred to another metal with substantially different mechanical properties but a similar golden appearance. Notably, numerous jewellery items like finger rings, solid bangles and chains continued to be produced only in copper or iron, even after the advent of gold working. Other jewellery items, like wrapped beads and wound helices continued to be made in copper and iron, along side production of similar items in gold and bronze. Bronze and gold may have been used interchangeably, to add their yellow colour to the pre-existing palette of the white of iron and the red of copper. There is ample evidence of the ritual significance of colour in African metal work, although the indigenous significance of gold has always been overshadowed by that of copper (Herbert 1984).

CONCLUDING REMARKS

Gold was produced mainly for export, and gold jewellery and insignia were associated only with the ruling elite who controlled this trade (Miller *et al.* 2000). It is likely that there was a hierarchy of access to various metals (Calabrese 2000), reflecting the hierarchy of social status that characterised settlement patterns in the Late Iron Age of southern Africa (Huffman 1996). The fabrication technology employed in working iron, copper, gold and bronze in jewellery was substantially uniform and remarkably stable through time, with minor variations made possible because of the enhanced malleability of gold. Deliberate alloying of gold was not performed, nor was refining to remove silver. Soldering and gold casting into moulds was unknown. The fabrication technology employed for gold (and bronze) developed linearly from that employed for the previous 1000 years in working copper and iron (Miller 2002), which points to the indigenous nature of this technology, with no significant external input. A simple, rudimentarily tool kit was used with great manual skill to produce delicate items of jewellery that embodied the stability and continuity of a local indigenous African style of metal working.

ACKNOWLEDGEMENTS

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Table 1. Selected gold artefacts from Mapungubwe described metallographically.

Object	Structure	Constituents	Alloy
M1231 A annular bead, 0.191 g	wrapped bead, visible open join, diameter 3.5 mm, thickness 2.2 mm	homogeneous, bulk of material has angular recrystallised equi-axed grains with annealing twins Hv 48 (n=3, range 45–51)	4.0% Ag
M1231 B annular bead, 0.099 g	wrapped bead, visible open join, diameter 3.2 mm, thickness 1.5 mm	homogeneous, bulk material consists of recrystallised angular, equi-axed grains with annealing twins Hv 67 (n=2, range 66–67)	4.5% Ag
M1231 C annular bead, 0.041 g	no visible join, diameter 2.1 mm, thickness 1.0 mm	homogeneous, recrystallised angular equi-axed grains, numerous bent annealing twins Hv 56 (n=3, range 55–56)	6.4% Ag
M1231 D annular bead, 0.037 g	no visible join, large serpentine voids, diameter 1.9 mm, thickness 1.0 mm	homogeneous, recrystallised angular equi-axed grains, 4 stress fractures running through the cross section of the sample corresponding to punch marks	6.0% Ag
M1231 E annular bead, 0.045 g	no visible join, diameter 2.1 mm, thickness 1.3 mm	homogeneous, recrystallised angular equi-axed grains with a few bent annealing twins, voids on inner margin	10.2% Ag
M1231 F grooved bead, 0.201 g	punched bead with pentagonal shaped hole and 5 outer grooves, diameter 3.4 mm, thickness 2.0 mm	recrystallised angular equi-axed grains with straight twins and numerous slip bands Hv 58 (n=2, range 47–69)	12.4% Ag
M1231 G grooved bead, 0.043 g	no visible join, diameter 2.2 mm, thickness 1.1 mm	homogeneous, recrystallised angular equi-axed grains, two voids on inner margin closest to two of the grooves and the third one is in the bulk	5.0% Ag
M1231 H spherical prill, 0.555 g	numerous casting voids, diameter 4 mm	rounded dendritic grain structure, numerous inter-dendritic pores Hv 21 (n=1)	3.0% Ag
M1231 I helical strip fragment, 0.221 g	narrow flat strip, rough inner surface and smooth outer surface, length 13.5 mm, width 1.5 mm, thickness 0.3 mm	homogeneous, recrystallised angular equi-axed grains with annealing twins	3.9% Ag

Grain Size	Deformation	Fabrication
ASTM 6–7	join area: grains elongated, severely cold worked outer margin: smeared layers, grain elongation inner margin: grains squeezed together, few cracks & protuberances that have been flattened by stringing wear	strip cut from hammered sheet, annealed, wrapped around and join worked cold, outer margin cold worked through use wear
ASTM 5	join area: grains elongated outer margin: minor localised smearing and cold work deformation inner margin: some lamination and deformation due to smearing, slip bands in grains on inner margin	strip cut from hammered sheet, annealed, strip hammered around cold preserving rough inner surface, join hammered closed, outer surface burnished through use wear
ASTM 4	outer margin: many slip bands and elongated grains bulk: few slip bands inner margin: two voids diagonally opposite each other, some smearing	cast droplet, ends flattened, perforated with sharp-sided punch, annealed, cold working due punching and use wear
ASTM 5–6	outer margin: grain elongation and slip bands due to cold work bulk: 4 stress fractures correspond to corners of square punch, numerous slip bands inner margin: burnished, some smearing	cast droplet, ends flattened, perforated cold with sharp-sided square punch, smearing on inner margin and grain elongation on outer margin caused by use wear
ASTM 6–7	outer margin: elongated grains with slip bands bulk: finer grains with bent annealing twins inner margin: 4 voids corresponding to punch marks and elongated grains, smearing from stringing wear	cast droplet, ends flattened, punched cold with sharp-sided square punch, outer margin smeared due to use wear
ASTM 5	outer margin: severe deformation and grain flattening in base of grooves bulk: slip bands throughout due to heavy cold work inner margin: severe grain deformation and flattening, lamination due to smearing, originally round hole deformed into pentagonal shape by the indentation of the 5 external grooves	cast droplet, end flattened, perforated, 5 ornamental grooves impressed cold onto outer margin causing deformation and distortion of inner bore, slip bands due to pervasive cold work
larger grains in bulk: ASTM 5 smaller grains on margins: ASTM 10	outer margin: elongated flattened grains, 5 grooves with associated slip bands inner margin: lamination from smearing in use	cast droplet, ends flattened, perforated cold, briefly annealed, 5 grooves impressed cold onto outer margin, inner margin smoothed by use wear
–	none – no cold work	cast droplet, no further working
ASTM 6–7	inner margins rough, outer margins smooth, no visible deformation	hammered sheet on rough anvil, strip cut from ‘inside’ forming trapezoidal cross section, wrapped around (missing) fibre core, outer surface burnished

Objects	Structure	Constituents	Alloy
M1231 J helical strip fragment 0.175 g	narrow flat strip, wound into coil, length 10 mm, width 1.5 mm, thickness 0.3 mm	homogeneous, recrystallised angular equi-axed grains with straight annealing twins	3.8% Ag
M1231 K helical strip fragment, 0.090 g	narrow flat strip, both sides rough, length 12.5 mm, width 2.0 mm, thickness 0.3 mm	homogeneous, recrystallised angular equi-axed grains, a few voids and annealing twins present	3.1% Ag
M1231 L flat strip fragment, 0.089 g	narrow flat strip, rough inner surface and smooth outer surface, length 11.5 mm, width 1.6 mm, thickness 0.3 mm	homogeneous, recrystallised angular equi-axed grains with annealing twins	3.6% Ag
M1231 M flat sheet fragment, 0.037 g	narrow flat sheet, two kinks in sheet representing a fold, thickness 0.2 mm	homogeneous, recrystallised angular equi-axed grains; no slip bands but many bent annealing twins, 2 areas of intergranular corrosion	6.9% Ag
M1231 N tack, 0.062 g	flattened head, two longitudinal cracks in shaft, head diameter 1.5 mm, length 4.8 mm	homogeneous, recrystallised cold worked grains, numerous slip bands, longitudinal cracks	3.9% Ag
M1231 O tack, 0.045 g	flattened head, two longitudinal cracks in shaft, head diameter 1.4 mm, length 4.8 mm	homogeneous, recrystallised cold worked grains, numerous slip bands	4.1% Ag
M1231 P helical wire fragment, 0.155 g	coiled D-shaped wire, length 15 mm, diameter 0.5 mm, diameter of helix 2 mm	homogeneous, recrystallised angular equi-axed grains with annealing twins; no slip bands	8.3% Ag
M1231 Q helical wire fragment, 0.042 g	coiled D-shaped wire, length 9.2 mm, width 0.5 mm	homogeneous, recrystallised angular equi-axed grains with annealing twins; no slip bands	8.8% Ag
UCT C tack, 0.111 g	small headed tack, length 8.9 mm	homogeneous, heavily cold worked grains	4.4% Ag
UCT D tack, 0.135 g	headless tack, length 7.1 mm	homogenous, heavily cold worked grains	6.8% Ag

Grain Size	Deformation	Fabrication
ASTM 5–6	no visible deformation	hammered sheet on rough anvil, strip cut from 'inside' forming trapezoidal cross section, wrapped around core, outer surface burnished
ASTM 3	some minor local grain deformation	hammered sheet on rough anvil, strip cut from one side forming trapezoidal cross section, annealed, wound around core to form coil
ASTM 4	outer surface: smooth, no visible deformation bulk: annealing twins, no slip bands inner surface: rough, numerous pits and protuberances from hammering on a rough anvil.	hammered sheet on rough anvil, strip cut from 'inside' forming trapezoidal cross section, outer surface burnished, final anneal
ASTM 8	outer surface: burnished bulk: bent annealing twins, small grain size	hammered sheet on rough anvil, annealed, cut, bent
inner grains: ASTM 5–6 outer grains: ASTM 6–8	head: severe cold working sides of shaft: one side smooth, other side smeared bulk of shaft: two voids from tip to centre of nail, heavily cold worked grains	annealed wire hammered into 4-sided wedge incorporating longitudinally running voids, short length cut off with chisel, tapered by hammering cold, head formed by hammering into substrate cold
ASTM 8–9	head: severe cold working sides of shaft: one side smooth, other side smeared bulk of shaft: two voids from tip to centre of nail, heavily cold worked grains	anealed wire hammered into 4-sided wedge incorporating longitudinally running voids, short length cut off with chisel, tapered by hammering cold, head formed by hammering into substrate cold
ASTM 4–5	flattened outer margins of the coil due to wear	hammered wire, coiled, outer margins flattened by abrasion producing D-shaped cross-section, final anneal (accidental?)
ASTM 4–5	flattened outer margins of the coil due to wear	hammered wire, coiled, outer margins flattened by abrasion producing D-shaped cross-section, final anneal (accidental?)
ASTM 4–5	head: heavily cold worked, flattened elongated grains, voids on outer edge sides of shaft: one smooth, other smeared shaft: heavily cold worked throughout, slip bands, few bent twins, elongated, flattened grains in bulk of material	annealed wire hammered into 4-sided wedge incorporating longitudinally running voids, short length cut off with chisel, tapered by hammering cold, head formed by hammering into substrate cold
centre: ASTM 7–8 edges: ASTM 5	thick end: void occurs at one edge, heavily cold worked flattened grains, not as heavily worked as UCT C shaft: elongated grains run along length of sample	wire hammered into 4-sided wedge incorporating longitudinally running voids, short length cut off with chisel, headless so probably unused

Object	Structure	Constituents	Alloy
UCT F sheet fragment, 0.368 g	flat sheet, with 6 holes along one edge	homogeneous, annealed recrystallised grains with straight annealing twins	5.5% Ag
UCT I1 large annular bead, 0.30 g	punched bead, diameter 4.0 mm, thickness 1.9 mm	homogeneous, annealed recrystallised grains with bent annealing twins, four punch indentations on one side Hv 72 (n=4, range 64-80)	10.9% Ag
UCT I2 large annular bead, 0.29 g	punched bead, diameter 3.5 mm, thickness 1.8 mm	homogenous, recrystallised grains with bent annealed twins in bulk of material	4.5% Ag
UCT J1 wrapped annular bead, 0.13 g	wrapped bead made from wrought wire with bevelled edges, diameter 4.5 mm, thickness 1.7 mm	homogenous, recrystallised grains with bent annealed twins and slip bands in bulk of material Hv 70 (n=3, range 69–74)	8.5% Ag
UCT J2 wrapped annular bead, 0.13 g	wrapped bead made from wrought wire with bevelled edges, diameter 4.5 mm, thickness 1.7 mm	homogeneous, recrystallised grains with mostly straight annealing twins, several voids	3.7% Ag
UCT Ka small annular bead, ca. 0.06 g	flat round bead, diameter 2 mm, no visible join	in homogeneous, numerous voids and stress fractures	8.9% Ag
UCT Kb small annular bead, ca. 0.06 g	flat round bead, diameter 2 mm, no visible join	homogenous, recrystallised grains with a few bent annealing twins in bulk of material	4.9% Ag
UCT Kc small annular bead, ca. 0.06 g	flat round bead, diameter 2 mm, no visible join	homogeneous, recrystallised grains with bent annealing twins	8.9% Ag
UCT Kd small annular bead, ca. 0.06 g	flat round bead, diameter 2 mm, no visible join	homogeneous, recrystallised grains with bent annealing twins	4.7% Ag

Grain Size	Deformation	Fabrication
ASTM 4–6	all edges are smeared, pitted on both sides	sheet hammering out on rough anvil, annealed, burnished on one side, punched with tack holes, some post-annealing deformation on surfaces
ASTM 5–10	outer margin: grains crumpled, flattened, elongated bulk: larger grain size, bent twins due to cold work inner margin: grains elongated	cast prill flattened on two sides, punched cold with sharp four-sided punch, annealed, margins deformed and cold worked through use
ASTM 5	outer margin: local smearing, incorporating long laminar voids bulk: bent annealing twins, some dendritic grain structure inner margin: flattened grains	cast prill flattened on two sides, punched cold with sharp four-sided punch, annealed, margins deformed and cold worked through use
ASTM 5–6	outer margin: grains crumpled, flattened and elongated bulk: bent annealing twins, slip bands inner margin: crumpled grains, most of slip bands occur here, two voids on edge cold working on outer and inner margins	strip cut from hammered sheet, annealed, bent around cold, use wear caused bent twins and damage on inner and outer margins
ASTM 6	outer margin: smearing caused voids, crumpled grains bulk: some bent annealing twins, one large longitudinally running void inner margin: lamination and cracks with many voids large voids near join, cold work around the join.	strip cut from hammered sheet, annealed, bent around cold, closure of join and use wear caused bent twins and damage on inner and outer margins
ASTM 5–6	outer margin: smeared layers, two stress fractures running through bulk to inner margin, several slip bands bulk: one large void, several smaller ones, few slip bands inner margin: generally smoother, one void running from outer to inner margin.	cut hammered wire incorporating voids, annealed, bent around cold, ends flattened, outer margin smeared due to use
ASTM 6–10	outer margin: smeared, flattened, elongated grains, one void bulk: bent annealing twins, slip bands inner margin: continuous voids parallel to circumference due to smearing	cut from hammered sheet or wire, annealed, bent around cold, use wear caused bent twins and damage on inner and outer margins
ASTM 7–10, outer half grains smaller than inner	outer margin: slip bands, elongated flattened grains, two voids due to smearing bulk: slip bands, bent annealing twins, elongated grains, one large void inner margin: smeared, one void, flattened elongated grains	cut from hammered sheet, annealed, bent around cold, use wear caused bent twins and damage on inner and outer margins
ASTM 6–10	outer margins: flattened, elongated grains, smeared edge bulk: larger grains, bent annealing twins, three voids inner margin: smearing from stringing wear, one void running into bulk of material	cut from hammered wire or sheet, annealed, bent around cold, use wear caused bent twins and damage on inner and outer margins

	Broederstroom 4th–6th C AD	Divuyu 6th–8th C AD	Nqoma 7th–11th C AD	K2 11th–13th C AD	Mapungubwe 13th C AD	Bosutswe 8th–15th C AD	Great Zimbabwe 14th–16th C AD	Thulamela 14th–17th C AD
Bangles		Fe	Fe, Cu	Fe, Cu,	Fe, Cu,	Fe	Cu, Cu/Sn	Fe, Cu,
Beads, punched					Au		Au	Au
Beads, wrapped	Cu, Fe	Cu, Fe	Cu, Fe	Cu	Fe, Cu, Au	Cu, Fe, Cu/Sn	Au, Cu	Au, Cu, Fe
Beads, rolled					Au		Au	
Chains		Cu, Fe	Cu, Fe					
Helices		Cu, Fe	Cu, Fe	Fe, Cu	Cu, Fe, Au, Cu/Sn	Cu, Cu/Sn, Fe, Au	Cu, Fe, Cu/Sn, Au	Fe, Cu/Sn, Au
Links	Cu, Fe	Cu, Fe	Cu, Fe		Au	Cu	Au	Fe
Loops		Fe			Cu		Cu	Cu
Pendants	Fe		Fe	Fe	Fe			
Rings			Fe	Cu		Fe		Cu
Sheet					Au		Au	Au, Cu, Fe, Cu/Sn
Tacks					Au		Au	Au, Cu/Sn

Table 2.

Metals and alloys used in jewellery from major sites spanning the Early and Late Iron Age in southern Africa, arranged in chronological sequence of appearance of novel metals. In the Early Iron Age and until the time of occupation of K2 (until the early thirteenth century AD) only copper and iron were in use. With the occupation of Mapungubwe (mid to late thirteenth century AD) gold and bronze appeared, and were present in all the assemblages dating from later levels at elite sites. There was a corresponding development in the technology, with the appearance at Mapungubwe of punched and rolled gold beads, and gold sheet and tacks, exploiting the malleability of this metal. (from Miller 2002).

6. SYSTEMATIC papers must conform to the International code of zoological nomenclature (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc. The name of the taxon should be followed, without intervening punctuation, by the author's(s') name(s) (not abbreviated) and the year of publication; a comma must separate author's(s') name(s) and year. The author's(s') name(s) and date must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be either according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order (see example 1), or according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry (see example 2). The author should adopt one style or the other throughout a paper.

Family **Nuculanidae**
Nuculana (Lembulus) bicuspidata (Gould, 1845)
Figs 14–15A

Example 1

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata (Gould) Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871, pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata (Gould): Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

NOTE punctuation in the above example: comma separates author's name and year; semicolon separates more than one reference by the same author; full stop separates references by different authors; figures of plates are enclosed in parentheses to distinguish them from text-figures; dash, not comma, separates consecutive numbers.

Example 2

1845	*Nucula (Leda) bicuspidata* Gould, p. 37.
1856	*Leda plicifera* A. Adams, p. 50.
1859	*Laeda bicuspidata* (Gould) Hanley, p. 118, pl. 228 (fig. 73).
1861	*Nucula largillierti* Philippi, p. 87.
1871	*Laeda bicuspidata* (Gould): Sowerby, pl. 2 (fig. 8a–b).
1950	*Leda bicuspidata* (Gould): Nicklès, p. 163, fig. 301.
1955	*Leda bicuspidata* (Gould): Nicklès, p. 110.
1964	*Leda bicuspidata* (Gould): Barnard, p. 234, figs 8–9.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated allotype (if applicable) and/or paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype. SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33 51 S 25 39 E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text, e.g. '… the Figure depicting *C. namacolus* …', or '… in *C. namacolus* (Fig. 10) ….'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names: e.g. Du Toit, but A. L. du Toit; Von Huene, but F. von Huene

(c) Scientific names, but not their vernacular derivatives e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary. Reference to the author should preferably be expressed in the third person. **Roman numerals** should be converted to arabic, except when forming part of the title of a book or article, e.g. 'Revision of the Crustacea. Part VIII. Amphipoda.'. A **specific name** must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter (except at the beginning of a sentence or paragraph), provided the same generic name is used consecutively. The name of **new genus or species** should not be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of *Biological Abstracts*.

8. GENERAL. Once referees' reports have been received by the editor, these will be discussed by the editorial committee. If the paper is considered acceptable after minor or major revision, the reports will be forwarded to the author who must then thoroughly revise in accordance with the referees' suggestions. Final acceptance of the revised manuscript will be considered by the editorial committee. In the case of major revision being necessary, the committee reserves the right to consult one or more referees regarding the revised manuscript.

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   - (b) *Abstract* of not more than 200 words, intelligible to the reader without reference to the text
   - (c) *Table of contents* giving hierarchy of headings and subheadings
   - (d) *Introduction*
   - (e) *Subject matter* of the paper, divided into sections to correspond with those given in table of contents
   - (f) *Summary* (if paper is lengthy)
   - (g) *Acknowledgements*
   - (h) *References*
   - (i) *Abbreviations*, where these are numerous.

3. MANUSCRIPT should be typed, double spaced with adequate margins. Four copies should be provided. First lines of paragraphs should be indented. Tables and a list of figure captions should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

   Major headings of the paper are centred capitals; first subheadings are centred small capitals; second subheadings are shouldered small capitals; third subheadings are shouldered italics; fourth subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations. Footnotes should be avoided unless they are short and essential. All generic and specific names should be underlined or italicized.

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     'Smith (1969: 36, fig. 16) described …'
     'As described (Smith 1969*a*, 1969*b*; Jones 1971)'
     'As described (Haughton & Broom 1927) …'
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FISCHER, P. H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* **74**: 627–634.

KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) **2**: 309–320.

KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* **17** (4): 1–51.

THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungreise im westlichen und zentralen Süd Afrika ausgeführt in den Jahren 1903–1905* **4** (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* **16**: 269–270.

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THE ASTEROID FAUNA (ECHINODERMATA) OF MARION & PRINCE EDWARD ISLANDS

by

S. STAMPANATO

&

M. JANGOUX

The South African Museum forms part of Iziko Museums of Cape Town

The Annals of the South African Museum publishes original research articles, revisions and review articles in natural history (palaeontology, geology, entomology, herpetology, ornithology, mammalogy, and marine and freshwater biology), social history (anthropology, archaeology and history), and art.

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THE ASTEROID FAUNA (ECHINODERMATA) OF MARION AND PRINCE EDWARD ISLANDS

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(With 2 figures and 1 table)

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ABSTRACT

Thirty-one species of asteroids were collected in waters off Marion and Prince Edward (MPE) islands during benthic surveys made by the University of Cape Town between 1982 and 1989. From the thirty-one species, one is new to science (*Solaster dianei* sp. nov.), eleven are new for the MPE area and eight were previously known only from the Subantarctic part of the Weddell quadrant.

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INTRODUCTION

The asteroid material on which the present report is based was collected between 5 m and 644 m depth near Marion and Prince Edward Islands (approximately 47°S, 37°E) during repeated benthic surveys carried out in 1982–9 by the University of Cape Town (UCT), South Africa.

The asteroid fauna of Marion and Prince Edward Islands (MPE) is poorly known. Twenty species are known to occur in the area mostly as a result of various scientific expeditions such as the Challenger Expedition (Sladen 1889), the Discovery Expedition (Fisher 1940; see also A.M. Clark 1962 [*Henricia fisheri*]), and the MPE South African Expeditions in 1965–6 and 1972–3 (Bernasconi 1968, 1971; Rowe and Clark 1975; respectively). Additional comments on some Marion asteroids species were also made by Jangoux (1982) and O'Loughlin & O'Hara (1990) (*Tremaster mirabilis* and *Smilasterias scalprifera*, respectively). The 1982–9 UCT benthic surveys collected thirty-one different species of asteroids, of which one is new to science and eleven are new for the MPE area. All the species known from previous expeditions were collected again but one, the korethrasterid *Peribolaster folliculatus* (taken by the Discovery).

Of the eleven species new for the MPE area, one was already known from the Enderby quadrant in the Subantarctic (viz. *Labidiaster annulatus*, a species that commonly occurs in Antarctic seas) and two were previously reported from Antarctic seas (*Solaster regularis* and *Odontaster validus*). The remaining nine species have a Subantarctic distribution and were previously recorded either both in the Weddell and Victoria quadrants (*Henricia obesa*) or in the Weddell quadrant only (*Odontaster penicillatus*, *Ceramaster patagonicus*, *Hippasteria falklandica*, *Hippasteria hyadesi*, *Pseudarchaster discus*, *Henricia studeri* and *Anteliaster australis*).

LIST OF STATIONS (all species were collected by dredging)

Station number	Date	Locality		Depth	Comments
		Lat. S.	Long. E.		
MAD 1	29/08/84	46°53'04"	37°53'05"	90	Very muddy substrate, black muddy volcanic sand covered in bryozoan fragments.
MAD 2	29/08/84	46°39'15"	37°52'02"	105–145	Rocky, shelly and bryozoan beds.
MAD 6	01/09/84	46°48'00"	38°00'00"	50–55	Very rocky bottom.
MAD 8	02/09/84	46°42'06"	37°48'05"	250–260	
MAD 12	16/04/85	46°45'00"	37°55'00"	150–152	
MAD 13	17/04/85	46°59'00"	37°47'05"	100–180	Muddy bottom.
MAD 15	21/04/85	46°35'00"	37°56'00"	48–50	
MAD 16	23/04/85	46°51'00"	38°04'00"	160–170	Sandy bottom dominated by polychaetes.

MAD 17	24/04/85	46°41'20"	37°49'00"	335–375	Very rocky bottom.
MAD 18	25/04/85	46°43'05"	38°01'00"	224–232	
MAD 20	26/04/85	46°49'00"	37°41'05"	34–42	Rocky and algae bottom.
MAD 21	29/04/85	47°01'02"	37°56'04"	349–351	Rocky bottom.
MAD 25	20/04/87	46°49'92"	37°53'95"	138–140	Fairly muddy bottom (lighter soil).
MAD 27	26/04/87	46°46'90"	38°00'00"	92–133	Light sandy bottom with volcanic rock.
MAD 28	28/04/87	46°43'58"	37°55'98"	237–243	Dark sediment.
MAD 29	28/04/87	46°41'25"	37°56'92"	143–147	Very muddy bottom covered in bryozoans.
MAD 31	04/05/87	46°53'92"	37°54'82"	42–85	Little sediment, red algae bottom.
MAD 32	07/05/87	46°49'35"	37°58'98"	147	Muddy bottom covered in bryozoan fragments.
MAD 37	24/08/87	46°40'55"	37°50'98"	460–488	Rocky bottom (large rocks).
MAD 38	25/08/87	46°57'88"	37°58'82"	190–210	Muddy bottom covered in bryozoan fragments.
MAD 39	26/08/87	46°59'75"	38°00'65"	360–376	Very rocky bottom.
MAD 40	31/08/87	46°40'25"	37°50'98"	375–462	Mixture of small pebbles and coarse gravel; little true sediment and no sand.
MAD 42	01/09/88	46°40'32"	37°51'00"	460–560	Rocky bottom, no sediment.
MAD 43	02/09/88	46°40'22"	37°51'20"	350–600	Rocky slope: large volcanic rocks, no sediment.
MAD 44	03/09/88	46°40'58"	37°50'20"	410–644	Rocky bottom, no sediment (slope area).
MAD 47	08/09/88	46°58'21"	37°52'00"	52–53	Muddy bottom (fine sediment).
MAD 48	05/09/88	46°58'68"	37°52'05"	92–105	Muddy bottom covered in bryozoan fragments.
MAD 49	07/09/88	47°00'35"	37°53'90"	265–306	Mud and rock substratum.
MAD 52	22/04/89	46°54'95"	37°34'15"	340–400	Very rocky bottom little sediment.
MAD 54	23/04/89	46°54'92"	37°35'00"	70–135	Coarse sediment with tiny volcanic rocks.
MAD 55	23/04/89	46°55'08"	37°35'20"	42–47	Very rocky; medium size pebbles and coarse gravel.
MAR 16	1982	46°51'03"	37°51'00"	10	Inshore collection at Transvaal Cove.
TP 5–8	1988	46°53'04"	37°52'03"	10	Diving survey at Trypot Point.
TVL 1–4	1988	46°51'03"	37°51'00"	5	Diving survey at Transvaal Cove.
TVL 5–8	1988	46°51'03"	37°51'00"	10	Diving survey at Transvaal Cove.
BB 1–4	1988	46°54'06"	37°54'04"	5	Diving survey at Bullards Bay.
BB 5–8	1988	46°54'06"	37°54'04"	10	Diving survey at Bullards Bay.

LIST OF COLLECTED SPECIES

The number of specimens and, when relevant, their measurements are indicated between brackets. Species new for the area are indicated in bold; an * means that the species is discussed below. R = length of the longest arm (radius); r = length from disc centre to interradius.

Families and species	Stations and numbers of individuals
ASTROPECTINIDAE	
Bathybiaster loripes Sladen, 1889	MAD 18 (2 juvenile)
Leptychaster kerguelenensis Smith, 1876	MAD 8 (1 juvenile); MAD 39 (1 juvenile)
ODONTASTERIDAE	
Acodontaster elongatus (Sladen, 1889)	MAD 12 (1 juvenile)
Odontaster meridionalis (Smith, 1876)	MAD 27 (1 juvenile); MAD 31 (2 : R/r mm = 21/10 & 47/18)
Odontaster penicillatus (Philippi, 1870)	MAD 44 (2 : R/r= 16/8 & 20/10 mm); MAD 31 (3 juvenile)
Odontaster validus Koehler, 1905	MAD 25 (3 : R/r mm [range] = 19–21/8:–12); MAD 43 (1: juvenile); MAD 37 (1 juvenile)
GONIASTERMAE	
****Ceramaster patagonicus*** (Sladen, 1889)	MAD 44 (1)
****Hippasteria falklandica*** Fisher, 1940	MAD 44 (1 : R/r mm = 73/27)
****Hippasteria hyadesi*** Perrier, 1891	MAD 42 (2 : R/r mm = 37/15 & 41/19)
****Pseudarchaster discus*** Sladen, 1889	MAD 39 (2 : R/r mm = 20/6 & 24/9)
ASTERINIDAE	
Tremaster mirabilis Verrill, 1879	MAD 44 (1 : R/r mm = 80/67 mm)
PORANIIDAE	
Porania antarctica Smith, 1876	MAD 1 (1 juvenile); MAD 29 (2 : R/r mm = 34/13 & 39/18); MAD 48 (3 : R/r mm [range] = 58–60/21–25)
ECHINASTERIDAE	
**Henricia fisheri* A.M. Clark, 1962	MAD 28 (1 : R/r mm = 44/7); MAD 44 (2 : R/r mm = 31/4 & 31/4) MAD 55 (1 : R/r mm = 34/6)
****Henricia*** sp. aff. ***H. obesa*** (Sladen, 1889)	MAD 44 (2: R/r mm = 37/8 & 48/10)
Henricia praetans (Sladen, 1889)	MAD 12 (1 juvenile); MAD 15 (7: R/r mm [range] = 10–15/3–5); TVL 1–4 (1: R/r mm= 12/3)

ECHINASTERIDAE *continued*	
**Henricia* sp. aff. *simplex* (Sladen, 1889)	MAD 1 (1 juvenile); MAD 6 (3 juvenile); MAD 38 (1 : R/r mm = 20/3)
****Henricia*** sp. aff. ***H. studeri*** (Perrier, 1891)	MAD 44 (1 : R/r mm = 36/6)
SOLASTERIDAE	
Crossaster penicillatus Sladen, 1889	MAD 16 (1 : R/r mm = 39/4); MAD 49 (1 : R/r mm = 37/4); MAD 28 (1 : R/r mm = 43/11); MAD 52 (1 juvenile)
Lophaster stellans Sladen, 1889	MAD 13(2 : R/r mm = 14/3 & 21/6)
****Solaster dianei*** nov. sp.	MAD 17 (1 : R/r mm = 59/18); MAD 43 (1 : R/r mm = 56/18)
****Solaster regularis*** Sladen, 1889	MAD 2 (1 : R/r mm = 61/31); MAD 44 (1 : R/r mm = 89/24); MAD 48 (1 : R/r mm = 62/18); MAR 16 (3 : R/r mm [range] = 47–59/17–26); TP 5–8 (8 : R/r mm [range] = 32–54/13–16); TVL 5–8 (1 juvenile); BB 5–8 (2: R/r mm = 60/16 & 92/25)
PTERASTERIDAE	
Diplopteraster semireticulatus (Sladen, 1882)	MAD 21 (1 : R/r mm = 48/31)
Pteraster affinis Smith, 1876	MAD 8 (1 : R/r mm = 61/20)
LABIDIASTERIDAE	
Labidiaster annulatus Sladen, 1876	MAD 8 (1 juvenile); MAD 40 (1 juvenile); MAD 43 (1 juvenile)
ASTERIIDAE	
Anasterias rupicola (Verrill, 1876)	MAR 16 (1 : R/r mm = 29/9)
****Anteliaster australis*** Fisher, 1940	MAD 12 (2 : R/r mm = 19/4 & 19/4).
Anteliaster scaber (Smith, 1876)	MAD 21 (1 juvenile); TVL 5–8 (1 juvenile); BB 1–4 (1 juvenile)
Diplasterias meridionalis (Perrier, 1875)	MAD 31 (1: R/r mm = 40/8); MAD 47 (1 : R/r mm [range] = 41/9); MAD 54 (3: R/r mm [range] = 23–44/6–10)
Pedicellaster hypernotius Sladen, 1889	MAD 12 (1 : R/r mm = 15/4)
Smilasterias scalprifera (Sladen, 1889)	MAD 47 (4 : R/r mm [range] = 74–82/8–11)
Smilasterias triremis (Sladen, 1889)	MAD 15 (2 : R/r mm = 18/4 & 18/4); MAD 20 (2 : R/r mm = 14/3 & 17/4); MAD 47 (9 : R/r mm [range] = 24–25/4–6); MAR 16 (2 : R/r mm = 20/5 & 29/6); TVL 1–4 (1 : R/r mm = 25/6)

TAXONOMICAL AND ZOOGEOGRAPHICAL COMMENTS

Ceramaster patagonicus (Sladen, 1889)

?*Astrogonium granulare* Whiteaves, 1887: 117 (according to Fisher 1911).

Pentagonaster patagonicus Sladen, 1889: 269, pl. 46 (figs 3–4); pl. 49 (figs 3–4).

Mediaster patagonicus Verrill, 1899: 145, 4 figs.

Pentagonaster austrogranularis Perrier, 1891: 127, pl. 12 (figs 3a–3b) (synonymized by Fisher 1940).

Ceramaster patagonicus Fisher, 1911: 214–6, pl. 37 (fig. 4), pl. 38 (figs 1–2), pl. 60 (fig. 3); 1940: 118. Koehler, 1923: 94. Djakonov, 1950: 48, figs 21, 88, 186. A.M. Clark, 1962: 23. Bernasconi, 1963: 8, pl. 1 (figs 1–2), pl. 2 (fig. 3); 1973: 297, pl. 7 (fig. 2). Tommasi, 1970: 12 (fig. 36). Codoceo & Andrade, 1979: 156, pl. 2 (figs 5–6).

Ceramaster patagonicus var. *euryplax* H.L. Clark, 1923: 262–4, pl. 14 (figs 1–2); 1926: 9–10. A.M. Clark, 1952: 195, 204–5.

Ceramaster chondriscus H.L. Clark, 1923: 258–60, pl. 14 (figs 5–6). Mortensen, 1933: 242 (synonymized by A.M. Clark 1974).

Ceramaster patagonicus productus Djakonov, 1950: 48.

Ceramaster patagonicus euryplax A.M. Clark, 1974: 435. A.M. Clark & Courtman-Stock, 1976: 61.

Though *Ceramaster patagonicus* has been rather frequently recorded over the past 100 years, its status needs examination mostly because of its puzzling distribution. The type locality is station 313 of the Challenger Expedition (Atlantic entrance to the Strait of Magellan; Sladen 1889). In the southern hemisphere, the species was found around the southernmost part of South America (New Year Sound, Cape Horn, Perrier 1891; Falkland plateau, Koehler 1923 and Fisher 1940; off South Argentina, Bernasconi 1963; off South Brazil, Tommasi 1976; off Central Chile, Codoceo & Andrade 1979) as well as off the Atlantic coast of South Africa (subspecies *euryplax*; see A.M. Clark & Courtman-Stock 1976). The species was also reported to occur in the N.E. Pacific (from the Gulf of California to south of the Alaskan Peninsula; Verrill 1899, Fisher 1911), in the southern portion of the Bering Sea (Djakonov 1950), and in the Okhotsk Sea (subspecies *productus*; Djakonov 1950).

Hippasteria falklandica Fisher, 1940

Hippasteria falklandica Fisher, 1940: 125, pl. 3 (fig. 2), pl. 4 (fig. 4). A.M. Clark, 1962: 22. Bernasconi, 1963: 15–6; 1973: 299–300, pl. 4 (figs 1, 4).

This is the third record of a species known only from two specimens, viz. the type specimen (type locality: Falkland Islands, 225–51 m; Fisher 1940) and an additional one originating from off Buenos Aires province, Argentina (Bernasconi 1973). The discovery of the species in the MPE area greatly extends its geographical distribution.

Although smaller than the holotype (R/r mm = 129/43 & 73/27 for the holotype and the MPE specimen respectively), the MPE specimen fits Fisher's original description rather well. The limits of abactinal plates are difficult to distinguish as they are not outlined by a row of closely appressed peripheral granules as in many other *Hippasteria* species. Abactinal plates with small scattered granules and with a well-developed bivalve pedicellaria (from 1.5 to 3.5 mm long) or one (mostly) or two globose tubercles.

Superomarginals are clearly marked off from the abactinals while inferomarginals are not easily distinct from the outer actinolaterals. Most marginal plates carry one or two bivalve pedicellariae and one to three globose tubercles. The terminal superomarginals gradually decrease in size instead of being larger than the subterminal plates as they are in the holotype. Most actinolateral plates bear a long bivalve pedicellaria; this is surrounded by enlarged squarish to polygonal granules. Adambulacral plates usually have two furrow spines (some proximal-most plates having only one) and two stouter subambulacral spines arranged transversally; these are surrounded by small, flattened, peripheral granules.

Hippasteria hyadesi Perrier, 1891

Hippasteria hyadesi Perrier, 1891: 128. Fisher, 1940: 125–6. A.M. Clark, 1962: 22. Bernasconi, 1963: 16–17, pl. 3 (fig. 2), pl. 5 (fig. 2). Codoceo & Andrade, 1979: 156, pl. 2 (figs 3–4).

The species was previously known from the type locality (Puerto Hambre, Magellan Strait, 36 m, 1 specimen; Perrier 1891) and from off central Chile (300–400 m, 6 specimens; Codoceo & Andrade 1979). Its discovery in the MPE area significantly extends its known geographical distribution.

The MPE specimens (R/r mm = 37/15 & 41/19) are slightly smaller than the holotype (R/r of the holotype: 50/9 mm; Bernasconi 1963) and much smaller than the largest recorded specimen whose R/r ratio is 144/62 mm (Codoceo & Andrade 1979). Abactinal plates are outlined by a distinct row of spaced peripheral granules. Both carinal and proximal-most adcarinal plates are enlarged and circular in shape; each plate bears a stout conical spine. Other abactinal plates are quadrangular to pentagonal in shape. They bear either one (sometimes two) globose tubercules or a well developed bivalve pedicellaria. Small secondary triangular abactinal plates occur in the disc centre between some of the most proximal carinal and adcarinal plates. Superomarginals and inferomarginals are clearly distinct from the abactinal and actinolateral plates. Marginals, outlined by closely appressed granules, bear from one to three stout conical spines (neither bivalve pedicellariae nor globose granule occur on these plates). Actinolateral plates are outlined by small flattened granules; the actinolaterals lining the adambulacral plates usually have one bivalve pedicellaria while others bear one or two globose to squarish tubercles. Adambulacral plates with usually one (two on the most proximal) elongated furrow spines and one shorter conical subambulacral spine.

Pseudarchaster discus Sladen, 1889

Pseudarchaster discus Sladen, 1889: 110, pl. 19 (figs 1–2), pl. 42 (figs 3–4). Fisher, 1940: 117. A.M. Clark, 1962: 23. Bernasconi, 1963: 5–7, pl. 2 (figs 1–2), pl. 4 (fig. 2). Codoceo & Andrade, 1979: 157, pl. 3 (figs 1–2).
Astrogonium patagonicum Perrier, 1891: 125, pl. 13 (figs 2a–b) (synonymized by Fisher 1940).

That species was already known from various samples collected in the Magellan and Falkland areas as well as off Argentina (Rio de la Plata) and off central Chile. It is now reported from the Subantarctic part of the Enderby quadrant. Although these are smaller than most specimens previously sampled (R of the holotype = 30 mm), the MPE specimens agree well with Sladen's (1889) original description; the present specimens have well marked postadambulacral fascioles.

Genus *Henricia* Gray, 1840

In his report on the asteroids collected by the Discovery Expedition, Fisher (1940, p. 162) wrote that 'the name *Henricia* is applied to a considerable number of extremely unstable entities, for convenience called species'; the situation today remains almost unchanged. Twelve Antarctic and Subantarctic species of *Henricia* have been described based, in most cases, on vague or poorly established criteria. As, moreover, *Henricia* species show high intraspecific variability (e.g. Madsen 1987) identifications are rather uncertain, the geographical origins of the specimens being sometimes the only objective parameter that can be used (see A.M. Clark 1962). There is an obvious need for a careful revision of the southern species of *Henricia.*

Henricia fisheri A.M. Clark, 1962

Henricia simplex (pars) Sladen, 1889: 547–8 (only station 148).
Henricia simplex Fisher, 1940: 168–169, pl. 11 (fig. 3).
Henricia fisheri A.M. Clark, 1962: 46, text-fig. 5i, pl. 2 (figs 3, 6).

Henricia fisheri is one of the few well-defined southern species of *Henricia.* It has been described by A.M. Clark (1962) from Crozet and Marion specimens previously identified as *Henricia simplex* by Sladen (1889) and Fisher (1940), respectively. The individuals have a rather small-meshed abactinal skeleton, most meshes containing three to four papulae. Abactinal spinelets are single, well separate from each other, and sheathed in skin. As reported by A.M. Clark (1962), the actinal and inferomarginal plates are very regularly arranged in longitudinal series (no actinal papulae were observed on the MPE specimens). Adambulacral plates bear three to five subambulacral spinelets arranged in a single transverse series.

Henricia sp. aff. *Henricia obesa* (Sladen, 1889)

Cribrella obesa Sladen, 1889: 544–5, pl. 96 (figs 3–4), pl. 98 (figs 5–6).
Cribrella hyadesi Perrier, 1891: 100–102, pl. 9 (figs 1a–d), pl. 10 (fig. 2).
Henricia hyadesi H.L. Clark, 1910: 336, pl. 2 (fig. 5).
Henricia hyadesi H.L. Clark, 1916: 60; 1946: 148.
Henricia pagenstecheri (pars) Koehler, 1923: 60 (according to Fisher 1940).
Henricia obesa Fisher, 1940: 164–6, pl. 11 (fig. 2). Mortensen, 1941: 3, pl. 1 (fig. 3). Madsen, 1956: 30; 1965: 169. A.M. Clark, 1962: 48–9, text-figs 5n–6a–c. Bernasconi, 1966: 169; 1973: 308; 1980: 250, pl. 1 (figs 3–4). Hernandez & Tablado, 1985: 4–5, fig. 1a–b. Rowe & Albertson, 1987: 190–2, fig 2a–b.

The species is known mostly from the Subantarctic part of the Weddell quadrant. It is also reported off Macquarie Island and off South Australia (Rowe & Albertson 1987). The MPE specimens have a rather large-meshed abactinal skeleton, with one to four papulae per mesh. Inferomarginal plates with ten to twelve spinelets. Actinolateral plates with two to six spinelets: four to six spinelets on the most proximal plates; two spinelets on the most distal ones. Only the innermost actinolateral series reaches the arm tips. Papulae widespread actinolaterally. Adambulacral armature made of six to seven spinelets arranged in bifid ('Y') series.

Henricia sp. aff. *Henricia simplex* (Sladen, 1889)

Cribrella simplex Sladen, 1889: 547, pl. 97 (figs 5–6), pl. 98 (figs 9–10).
Henricia simplex Mortensen, 1941: 2. A.M. Clark, 1962: 37.

As papulae occur between the proximal actinolateral plates, the MPE specimens belong to the *pagenstecheri* group. The last includes three species—viz. *Henricia pagenstecheri* (Studer, 1885), *Henricia simplex* (Sladen, 1889), and *Henricia lukinsi* (Farquhar, 1898)—that are almost indistinguishable from each other except in considering their type localities (see A.M. Clark 1962). Because of their relatively small-meshed abactinal skeleton, the MPE specimens are tentatively identified *Henricia simplex,* a species already recorded in MPE waters (Sladen 1889).

Henricia sp. aff. *Henricia studeri* (Perrier, 1891)

Cribrella studeri Perrier, 1891: 102, pl. 9 (fig. 2).
Henricia studeri Fisher, 1940: 163, pl. 11 (fig. l). A.M. Clark, 1962: 38. Bernasconi, 1966: 169; 1980: 252–3, pl. 1 (figs 1–2). Codoceo & Andrade, 1979: 158, pl. 4 (figs 5–6).

The MPE specimen presumably belongs to *Henricia studeri,* a species recorded several times in the Magellan–Falkland area. Abactinal spinelets occur in clusters of ten to twelve spinelets that each have a multifid vitreous tip. Actinal and inferomarginal plates are linked by bar-like plates giving the actinal skeleton a regular transverse arrangement. Actinolateral plates with *c.* ten spinelets each, arranged in two rows. Papulae occur all over the actinal surface. Proximal adambulacral plates with two transverse series of spinelets with four to five spinelets in each series.

Solaster dianei sp. nov
Figs 1, 2

Material

SAM–A24025, between Marion and Prince Edward Islands (46°41'2" S–37°39'0" E), 335–375 m, 1 specimen (Holotype); SAM–A24009, off Prince Edward Island (46°40'2" S–37°51'2" E), 1 specimen (Paratype).

Etymology

Dedicated to Diane Gianakouras who oversaw the 1982–9 faunistic survey of the Marion and Prince Edward area.

Diagnosis

A species of *Solaster* with 7 triangular-shaped arms. Abactinal paxillae short, irregularly arranged except at the sides of arms where they form oblique transverse series. Superomarginal paxillae clearly larger than the most lateral abactinal paxillae. Actinolateral area fairly large with 4 rows of actinolateral plates at the base of the arms. Actinal surface of oral plates covered with spinelets.

Description of the holotype

Arms 7; R = 59 mm; r = 18 mm; R = 3.3 r; breadth of arms at base 12 mm. Disk large; arms triangular, tapering progressively towards their distal extremity. Interbrachial arcs acute. Abactinal surface convex; actinal surface flat (Figs 1A, B).

Most abactinal plates 3 to 4-lobed. Abactinal paxillae 0.1 to 0.3 mm in diameter, and spaced 1 to 3 times their width (Fig. 2A). Largest disk paxillae with a crown up to 25 short point- to blunt-tipped spinelets measuring 0.15 mm in length; paxillae of the mid-central part of arms with up to 20 spinelets. Basal parts of spinelets form a single paxilla united in a membrane. Generally 2 papulae present in each skeletal mesh. Paxillae irregularly arranged except on arm sides where they form regular oblique transverse series. Abactinal paxillae occurring close to inferomarginals small; they bear *c.* 11 very short spinelets.

Superomarginal paxillae enlarged, easily distinguishable from the most lateral abactinal ones (Fig. 2B); those of the most proximal part of the arm measure 0.3 mm in diameter and have up to 30 spinelets (0.25 mm in length). Inferomarginal plates 42, conspicuous, defining the ambitus; proximal plate with an enlarged fan-like, transversally compressed pseudopaxilla measuring 2.5 mm in length and 0.3 mm in breadth. Inferomarginal fans with 3 to 4 transversal rows of spinelets measuring up to 1.5 mm in length.

Actinal interradial areas fairly large with four series of actinolateral plates, the

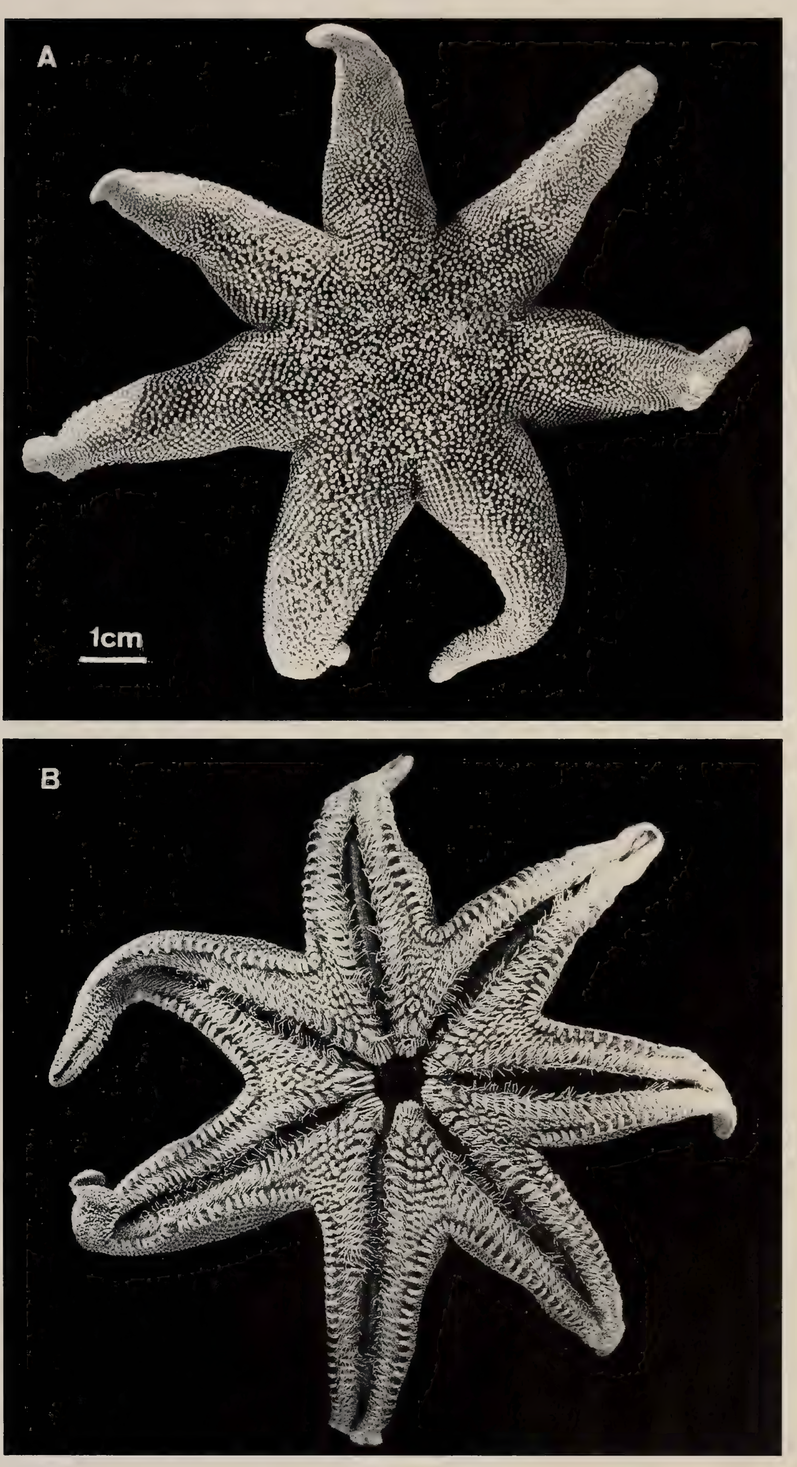

Figure 1
Solaster dianei nov. sp. Abactinal (A) and actinal (B) views of the holotype.

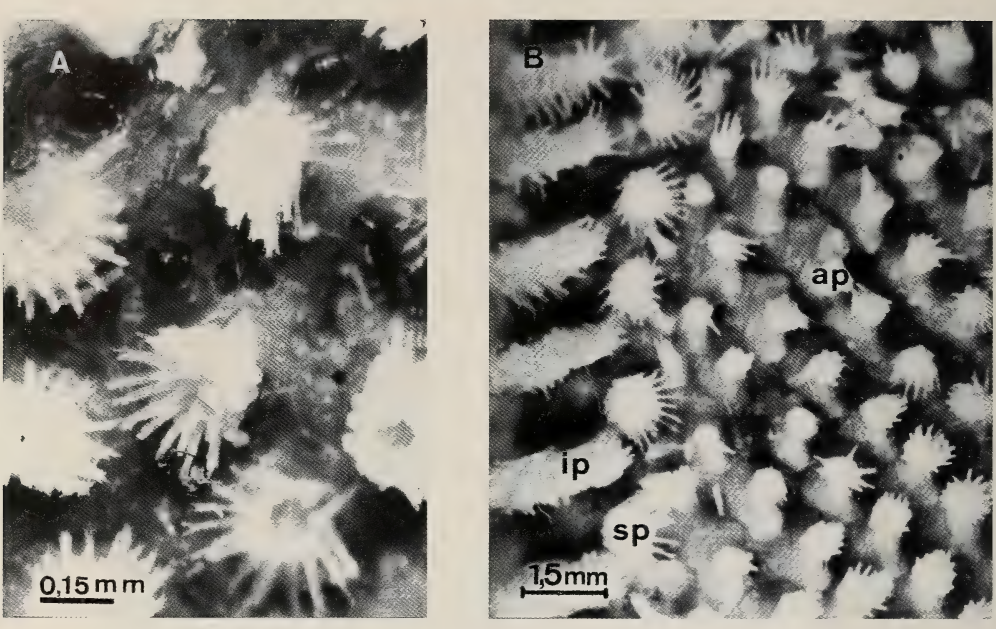

Figure 2
Solaster dianei nov. sp. (holotype). A. Abactinal paxillae of the disk central part. B. Profile view showing the abactinolateral (ap), superomarginal (sp) and inferomarginal (ip) paxillae.

innermost one extending half the arm length. Each actinolateral with a paxillar-like group of 4 to 8 spinelets up to 0.9 mm in length.

Adambulacral plates with 4 furrow spines webbed at their base, and 1 or 2 (most proximal plates) transverse combs of 6 to 7 subambulacral spines (*c.* 0.8 in length). Oral plates with 10 somewhat elongated furrow spines (maximal length: 1.5 mm), the surface of the plates being covered by up to 15 irregularly arranged shorter suboral spines.

Note on the paratype

R = 56 mm; r = 18 mm; R = 3.1 r. There are only slight differences between the two specimens, probably a result of size, viz. the paratype has 12 oral furrow spinelets (10 in the holotype) and up to 9 spinelets per subambulacral series (no more than 7 in the holotype).

Discussion

The species clearly belongs to the genus *Solaster*; it has a dense small-meshed abactinal skeleton and the abactinal paxillae on arm sides forms oblique transverse series. It basically differs from the southern species of *Solaster*—*S. torulatus* (Sladen, 1889) and *S. regularis* (Sladen, 1889)—in its extensive actinolateral areas, the occurrence of two distinct series of marginal plates, and the arrangement of the suboral spinelets on the oral plates.

Solaster regularis Sladen, 1889

Solaster regularis Sladen, 1889: 454, pl. 60 (fig. I), pl. 62 (figs 5–6). A.M. Clark, 1962: 50. Bernasconi, 1973: 309–10. Codoceo & Andrade, 1979: 157, pl. 3 (figs 5–6).
Solaster subarcuatus Sladen, 1889: 455–7, pl. 70 (fig. 2), pl. 72 (figs 7, 8). Doderlein, 1928: 296, pl. 12 (fig. 4).
Crossaster australis Perrier, 1891: 113, pl. 10 (figs la–ld) (synonymized by Fisher 1940).
Solaster octoradiatus Ludwig, 1903: 25–7, pl. 3 (figs 21–2). Bell, 1908: 11; 1917: 4. Jangoux & Massin, 1986: 91 (synonymized Fisher 1940).
Solaster australis Ludwig, 1905: 63. Fisher, 1911: 323 (synonymized by Fisher 1940).
Solaster regularis regularis Fisher, 1940: 178–9.
Solaster regularis subarcuatus Fisher, 1940: 179–80. A.M. Clark 1962: 55, text-figs 7o–s. McKnight, 1976: 28. Jangoux & Massin, 1986: 91.
Crossaster canopus H.E.S. Clark, 1963: 55, pl. 10 (figs 1–2), pl. 11 (synonymized by McKnight 1976).

According to Fisher (1940) two subspecies of *Solaster regularis* occur in the Southern Ocean, viz. *S. regularis regularis* from the Cape Horn region and the Falkland Plateau and *S. regularis subarcuatus* that is said to be ‘probably circumpolar’. The species, however, is known to be extremely variable (see e.g. Bernasconi 1973) and this is confirmed by the examination of the 18 specimens (size range: from 32 to 92 mm arm length) collected during the MPE Survey (Table 1). Indeed, though some specimens resemble either the *regularis* or *subarcuatus* subspecies, most show mixed features suggesting that Fisher’s subspecies might be artificial and may express the high polymorphism of the species.

Anteliaster australis Fisher, 1940

Anteliaster australis Fisher, 1940: 215–7, fig. I $_{\text{I–Id}}$, pl. 9 (figs 2–3). A.M. Clark, 1962: 72.

The species is closely related to *Anteliaster scaber* (Smith) from which it can be distinguished by more numerous abactinal pedicellariae (according to Fisher 1940), or by the size and shape of abactinal spinelets (according to A.M. Clark 1962). The abactinal spinelets have a bushy-headed form in *A. scaber* while they are shorter and truncated in *A. australis.* While the two abactinal features cited above (i.e. pedicellarial density and shape of abactinal spinelets) allowed recognition of the species in the MPE collection, their reliability as specific characters may be questionable (see A.M. Clark 1962, p. 72).

Table 1. Variations in number and shape of spinelets in *Solaster regularis*[1]

Type of spinelets	subspecies *regularis*	subspecies *subarcuatus*	MPE specimens
Number and shape of spinelets on abactinal paxillae	6 to 10 point-tipped spinelets	5 to 6 blunt-tipped spinelets	7 to 20 point- or blunt-tipped spinelets
Number of spinelets on inferomarginal paxillae	10 to 20	10 to 12	10 to 30
Number of spinelets on actinolateral plates	4 to 6	3 to 5	2 to 6
Number of furrow spinelets (adambulacral plates)	4 to 5	3 to 4	3 to 5
Number of subambulacral spinelets (adambulacral plates)	4 to 5	4 to 5	5 to 6
Number of furrow oral spinelets	9	8	7 to 11
Number of suboral spinelets	5	3 to 4	7 to 9

[1] Data from Sladen (1889) and Fisher (1940).

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J.H. DAY'S TYPE SPECIMENS OF POLYCHAETA (ANNELIDA) IN THE COLLECTION OF THE SOUTH AFRICAN MUSEUM

by

G.A. MARSKA

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by

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Natural History Division, South African Museum, Iziko Museums of Cape Town

(With 1 figure)

[*MS accepted May 1995*]

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INTRODUCTION

In 1990, the South African Museum (Marine Biology Department) received the entire J.H. Day reference collection of Polychaeta, previously housed in the Zoology Department, University of Cape Town. At the Museum, specimens were sorted, rebottled, preserved in 70 per cent ethanol and catalogued. Amongst the collection are the types of several species that were described by Day between 1934 and 1975. A list of these types is provided herein. In accordance with the recommendations of the *International Code of Zoological Nomenclature*, this paper forms part of the series of publications in *Annals of the South African Museum* documenting the South African Museum's holdings of type material.

The vast majority of type specimens were obtained by the Zoology Department of the University of Cape Town during extensive ecological surveys over a number of years. These surveys covered an area along the coast of southern Africa extending from Walvis Bay on the west coast to Mozambique on the east. For easy reference, a map of the area (Fig. 1) from Day (1967: 8), is included.

There are also a few type specimens from Western Australia, the United States, and India.

Ann. S. Afr. Mus. **112** (2), 2004:17–38, 1 fig.

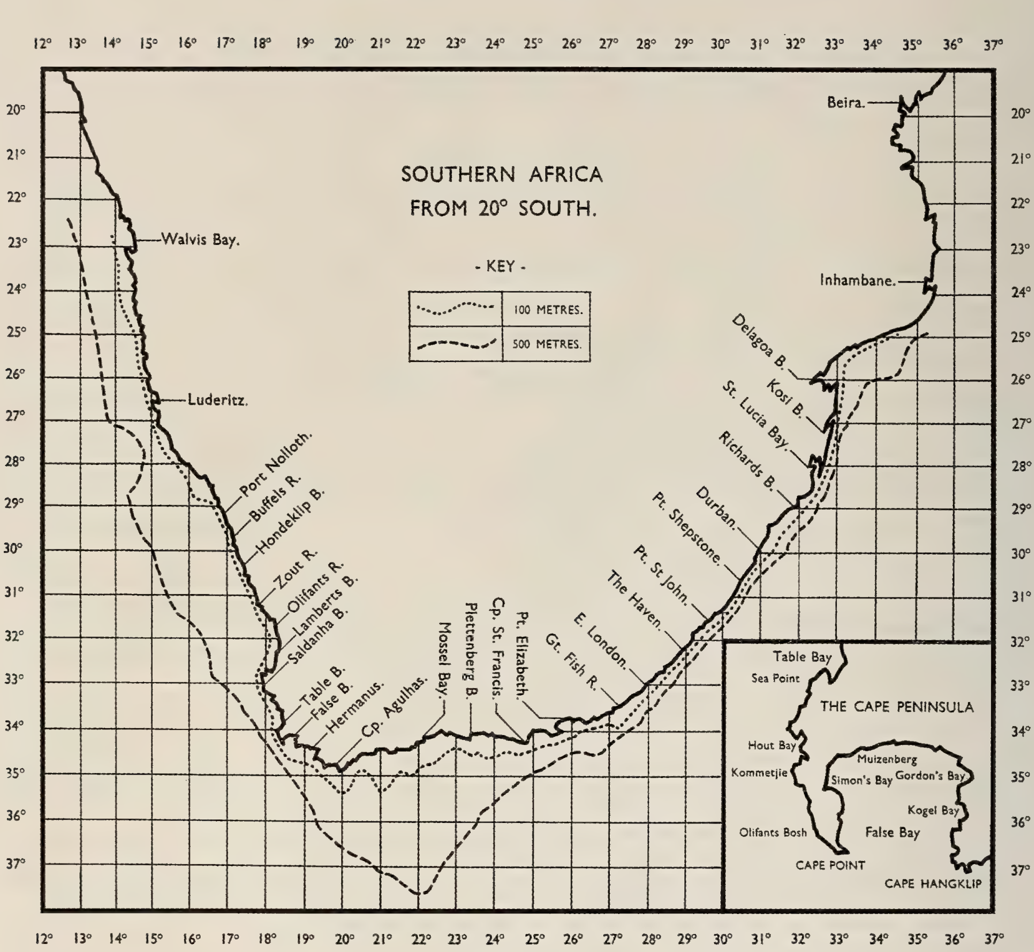

Figure 1

In addition to Day's publications, the South African Museum is in possession of some of his unpublished material, e.g. notes indicating types deposited in the South African Museum and Natural History Museum, London, and annotated card index of specimens. Pertinent information derived from these unpublished sources is included, where applicable, in 'remarks' at the end of the entry for each species.

The name under which a species was first described is placed in square brackets, if this name has since been changed. The current name appears in round brackets following the original reference.

If a valid species has been transferred from the original to another genus, the current name and reference is followed by the original name in round brackets.

The classification, species names and the spelling used herein as well as coordinates follow those used by Day in his publications.

ANNELIDA
POLYCHAETA
ERRANTIA
Family **Polynoidae**

Antinoe Kinberg, 1855

Antinoe lactea Day, 1953: 403.
Type status: Syntype: SAM–A20960.
Locality: Langebaan Lagoon, Cape west coast, South Africa.
Collected by: UCT Ecological Survey.

Specimen label refers to this specimen as a paratype; in his original description, Day did not formally designate types. Day's notes state 'lectotype in British Museum', and BM collection is reported to include syntypes.

Harmothoe Kinberg, 1855

Harmothoe gilchristi Day, 1960: 275.
Type status: Holotype: SAM–A20904.
Locality: 34°46'S 23°27'E, 110 metres (Cape south coast, South Africa).
Collected by: UCT Ecological Survey.

Harmothoe saldanha Day, 1953: 401.
Type status: Syntype: SAM–A20979.
Locality: Langebaan Lagoon, Cape west coast, South Africa.
Collected by: UCT Ecological Survey.

Harmothoe corralophila Day, 1960: 278.
Type status: Syntype: SAM–A20903.
Locality: 34°09,4'S 18°16,6'E, 75 metres (Cape west coast, South Africa).
Collected by: UCT Ecological Survey.

Harmothoe agulhana Day, 1960: 277.
Type status: Holotype: SAM–A20902.
Locality: 34°00,4'S 25°44,5'E, 39 metres (Algoa Bay, South Africa).
Collected by: UCT Ecological Survey.

Harmothoe profunda Day, 1963: 357.
Type status: Holotype: SAM–A19780.
Type status: Paratype: SAM–A21061.
Locality: 33°49'S 16°30'E, 2 745 metres (South Africa).
Collected by: UCT Ecological Survey (R.S. *Africana*).

Gattyana McIntosh, 1900

Gattyana mossambica Day, 1962: 629.

Type status: Paratype: SAM–A20980.
Locality: Inhaca Island, Mozambique.
Collected by: UCT Ecological Survey.
Remarks: In Day's unpublished notes, *Gattyana mossambica* is referred to as *Harmothoe* (*Gattyana*) *mossambica*.

Lepidonotus Leach, 1816

Lepidonotus (*Thormora*) *jolli* Day, 1975: 173.

Type status: Paratype: SAM–A21011.
Locality: Rottnest Island, Western Australia.
Collected by: L. Joll, 1972.

Pseudopolynoe Day, 1962

Pseudopolynoe inhaca (Day), 1951: 15 (as *Polynoe inhaca*).

Type status: Syntype: SAM–A20893.
Locality: Inhaca Island, Mozambique.
Collected by: UCT Ecological Survey.

Lepidasthenia Malmgren, 1867

Lepidasthenia mossambica Day, 1962: 632.

Type status: Paratype: SAM–A20981.
Locality: Inhaca Island, Delagoa Bay.
Collected by: UCT Ecological Survey.

Lepidasthenia brunnea Day, 1960: 285.

Type status: Syntype: SAM–A20925.
Type status: Syntype: SAM–A20953.
Locality: 34°23,3'S 18°40,3'E, 88 metres (False Bay, South Africa).
Collected by: UCT Ecological Survey.

Family **Sigalionidae**

Psammolyce Kinberg, 1855

Psammolyce articulata Day, 1960: 293.
Type status: Syntype: SAM–A20912.
Type status: Syntype: SAM–A20911.
Locality: Simons Bay, Cape west coast, South Africa.
Collected by: UCT Ecological Survey.

Sthenelais Kinberg, 1855

[*Sthenelais papillosa*] Day, 1960: 289 (transferred to *Fimbriosthenelais zetlandica* (McIntosh, 1876) by Pettibone 1971)).
Type status: Syntype: SAM–A21046.
Locality: 34°13,9'S 18°31,6'E, 40 metres (False Bay, South Africa).
Collected by: UCT Ecological Survey

Sigalion Audouin & Milne Edwards, 1832

Sigalion capense Day, 1960: 291.
Type status: Syntype: SAM–A20929.
Locality: 34°22,7'S 18°43,1'E, 79 metres (False Bay, South Africa).
Collected by: UCT Ecological Survey.

Family **Pisionidae**

Pisione Grube, 1856

Pisione africana Day, 1963*a*: 390.
Type status: Paratype: SAM–A21005.
Locality: 34°35'S 21°56'E, 78 metres (Cape south coast, South Africa).
Collected by: UCT Ecological Survey.

Family **Phyllodocidae**

Subfamily Phyllodocinae

Protomystides Czerniavsky, 1882

Protomystides capensis Day, 1960: 306.
Type status: Holotype: SAM–A20913.
Locality: 32°48'S 17°58'E, 9 metres (South Africa).
Collected by: UCT Ecological Survey.

Eulalia Savigny, 1818

Eulalia (*Sige*) *falsa* Day, 1960: 303.
Type status: Syntype: SAM–A20918.
Type status: Syntype: SAM–A20919.
Locality: 34°12,8'S 18°36,5'E, 46 metres (False Bay, South Africa).
Collected by: UCT Ecological Survey.

Family **Alciopidae**

Vanadis Claparede, 1870

Vanadis crystallina inornata Day, 1967: 182.
Type status: Paratype: SAM–A20937.
Locality: 30°16'S 31°49'E, 150–0 metres (off Natal, South Africa).
Collected by: UCT Ecological Survey.

Family **Hesionidae**

Ophiodromus Sars, 1861

Ophiodromus berrisfordi Day, 1967: 224.
Type status: Syntype: SAM–A20894.
Locality: Walvis Bay, Cape west coast, South Africa.
Collected by: UCT Ecological Survey.
Remarks: In Day's unpublished material, *Ophiodromus berrisfordi* is referred to as *Podarke berrisfordi*.

Family **Syllidae**

Subfamily Syllinae

Syllis Savigny, 1818

Syllis (*Haplosyllis*) *trifalcata* Day, 1960: 308.
Type status: Holotype: SAM–A20932.
Locality: 34°12,4'S 18°43,5'E, 41 metres (South Africa).
Collected by: UCT Ecological Survey.

Syllis (*Typosyllis*) *benguellana* Day, 1963*a*: 399.
Type status: Paratype: SAM–A20958.
Locality: 32°05,5'S 18°17,3'E, 27 metres (South Africa).
Collected by: UCT Ecological Survey.

Opisthosyllis Langerhans, 1879

Opisthosyllis laevis Day, 1957: 74.

Type status:	Paratype: SAM–A20944.
Locality:	Mozambique Island.
Collected by:	UCT Ecological Survey.

Trypanosyllis Claparede, 1864

Trypanosyllis ankyloseta Day, 1960: 312.

Type status:	Holotype: SAM–A20926.
Locality:	34°12,4'S 18°43,5'E, 42 metres (South Africa).
Collected by:	UCT Ecological Survey.

Subfamily Eusyllinae

Pionosyllis Malmgren, 1867

Pionosyllis magnidens Day, 1953: 416.

Type status:	Syntype: SAM–A21051.
Locality:	Lamberts Bay, Cape west coast, South Africa.
Collected by:	UCT Ecological Survey.

Lamellisyllis Day, 1960

Lamellisyllis comans Day, 1960: 319.

Type status:	Holotype: SAM–A20924.
Locality:	34°09,3'S 18°51'E, 8-12 metres (South Africa).
Collected by:	UCT Ecological Survey.

Family **Nereidae**

Dendronereides Southern, 1921

Dendronereides zululandica Day, 1951: 30.

Type status:	Syntype: SAM–A20940.
Locality:	St Lucia Estuary, South Africa.
Collected by:	UCT Ecological Survey.

Nereis Linnaeus, 1758

Nereis (*Neanthes*) *agulhana* Day, 1963*a*: 406.

Type status:	Paratype: SAM–A20982.
Locality:	34°03'S 25°59'E, 84 metres (South Africa).
Collected by:	UCT Ecological Survey.

Nereis (*Neanthes*) *indica brunnea* (Day), 1957: 80.
Type status: Syntype: SAM–A20983.
Locality: Morrumbene Estuary, east coast South Africa.
Collected by: UCT Ecological Survey.

Nereis (*Neanthes*) *mossambica* Day, 1957: 78.
Type status: Paratype: SAM–A20984.
Locality: Morrumbene Estuary, east coast South Africa.
Collected by: UCT Ecological Survey.

Nereis (*Neanthes*) *willeyi* Day, 1934: 39.
Type status: Syntype: SAM–A20985.
Locality: St James, Cape west coast, South Africa.
Collected by: UCT Ecological Survey.

Nereis (*Nereis*) *gaikwadi* Day, 1973*a*: 344.
Type status: Paratype: SAM–A21012.
Locality: Ratnagiri, south of Bombay, India.
Collected by: U.D. Gaikwad at Ratnagiri.

Ceratonereis Kinberg, 1866

Ceratonereis keiskama Day, 1953: 426.
Type status: Paratype: SAM–A20961.
Locality: Keiskama Estuary, Cape south coast, South Africa.
Collected by: UCT Ecological Survey.

Family **Nephtyidae**

Nephtys Cuvier, 1817

Nephtys (*Nephtys*) *capensis* Day, 1953: 431.
Type status: Syntype: SAM–A20987.
Locality: Paarden Island, Cape Peninsula, South Africa.
Collected by: UCT Ecological Survey.

Family **Glyceridae**

Glycera Savigny, 1818

Glycera natalensis Day, 1957: 86.
Type status: Paratype: SAM–A20978.
Locality: Durban (Surf Beach), South Africa.
Collected by: UCT Ecological Survey.

Family **Goniadidae**

Glycinde Muller, 1858

Glycinde capensis Day, 1960: 331.
Type status: Holotype: SAM–A20921.
Type status: Paratype: SAM–A20922.
Locality: 34°09,3'S 18°27,7'E, 22 metres (South Africa).
Collected by: UCT Ecological Survey.

Family **Onuphidae**

Diopatra Audouin & Milne Edwards, 1833

Diopatra dubia Day, 1960: 348.
Type status: Holotype: SAM–A20989.
Type status: Paratype: SAM–A20990.
Locality: 34°22,7'S 18°43,1'E, 79 metres (South Africa).
Collected by: UCT Ecological Survey.

Diopatra monroi Day, 1960: 345.
Type status: Holotype: SAM–A20996.
Type status: Paratype: SAM–A20991.
Locality: 32°09'S 18°06'E, 108 metres (South Africa).
Collected by: UCT Ecological Survey (R. S. *Africana* II).

Diopatra neapolitana var *capensis* Day, 1960: 344.
Type status: Syntype: SAM–A20992.
Type status: Syntype: SAM–A20993.
Locality: 33°58'S 25°43'E, 38,5 metres (South Africa).
Collected by: UCT Ecological Survey.

Epidiopatra Augener, 1918

Epidiopatra gilchristi Day, 1960: 352.
Type status: Holotype: SAM–A20917.
Locality: 33°03'S 27°56'E, 57 metres (South Africa).
Collected by: UCT Ecological Survey.

Epidiopatra hupferiana var *monroi* Day, 1957: 92.
Type status: Syntype: SAM–A21010.
Locality: 34°07'S 18°32,5'E, 18 metres (South Africa).
Collected by: UCT Ecological Survey.

Rhamphobrachium Ehlers, 1887

Rhamphobrachium capense Day, 1960: 355.
Type status: Holotype: SAM–A20933.
Type status: Paratype: SAM–A20934.
Locality: 34°07,5'S 18°31'E, 27.5 metres (South Africa).
Collected by: UCT Ecological Survey.

Family **Lumbrineridae**

Lumbrineris Blainville, 1828

Lumbrineris heteropoda difficilis Day, 1963*a*: 410.
Type status: Syntype: SAM–A20952.
Locality: 25°50'S 33°00'E (South Africa).
Collected by: UCT Ecological Survey (R. S. *Africana* II).

Lumbrineris hartmani (Day), 1953: 437 (as *Lumbriconereis hartmani*).
Type status: Syntype: SAM–A21048.
Locality: St James, Cape west coast, South Africa.
Collected by: UCT Ecological Survey.
Remarks: In Day's unpublished material, *Lumbrineris hartmani* is a synonym of *Lumbrineris dubeni* Kinberg, 1866.

Family **Arabellidae**

Drilognathus Day, 1960

Drilognathus capensis Day, 1960: 370.
Type status: Holotype: SAM–A20999.
Type status: Paratype: SAM–A21000.
Locality: 32°05'S 18°17,7'E, 29 metres (South Africa).
Collected by: UCT Ecological Survey.

Drilonereis Claparede, 1870

Drilonereis monroi Day, 1960: 365.
Type status: Syntype: SAM–A21001.
Type status: Syntype: SAM–A21002.
Locality: 32°09'S 18°06'E, 108 metres (South Africa).
Collected by: UCT Ecological Survey (R. S. *Africana* II).

Notocirrus Schmarda, 1861

Notocirrus australis Day, 1960: 367.

Type status: Syntype: SAM–A20936.
Locality: 34°09,3'S 18°27,7'E, 22 metres (South Africa).
Collected by: UCT Ecological Survey.

SEDENTARIA

Family **Spionidae**

Boccardia Carazzi, 1895

Boccardia pseudonatrix Day, 1961: 493.

Type status: Holotype: SAM–A20970.
Type status: Paratype: SAM–A20969.
Locality: Knysna Heads, Cape south coast, South Africa.
Collected by: UCT Ecological Survey.

Nerinides Mesnil, 1896

Nerinides gilchristi Day, 1961: 491.

Type status: Paratype: SAM–A20931.
Locality: 33°06,5'S 17°55,4'E, 86 metres (South Africa).
Collected by: UCT Ecological Survey.
Remarks: In Day's unpublished material, *Nerenides gilchristi* is referred to as *Scololepis* (*Nerinides*) *gilchristi.*

Prionospio Malmgren, 1867

Prionospio cirrobranchiata Day, 1961: 488.

Type status: Holotype: SAM–A20955.
Locality: Off Saldanha Bay (South Africa)
Type status: Paratype: SAM–A20910.
Locality: 34°11'S 18°13'E, 144 metres (South Africa).
Collected by: UCT Ecological Survey.

Prionospio saldanha Day, 1961: 485.

Type status: Holotype: SAM–A21006.
Locality: Langebaan, Cape west coast, South Africa.
Type status: Paratype: SAM–A20909.
Locality: 33°03,5'S 18°01,5'E, 9 metres.
Collected by: UCT Ecological Survey.

Family **Magelonidae**

Magelona Muller, 1858

Magelona capensis Day, 1961: 495.
Type status: Holotype: SAM–A20897.
Locality: 34°37'S 21°56'E, 86 metres (South Africa).
Collected by: UCT Ecological Survey.
Remarks: Day (1961) designated the single specimen from the above locality as the holotype. However, the specimen label states paratype.

Family **Cirratulidae**

Subfamily Cirratulinae

Dodecaceria Oersted, 1843

Dodecaceria pulchra Day, 1955: 418.
Type status: Paratype: SAM–A20942.
Locality: Kalk Bay, Cape west coast, South Africa.
Collected by: UCT Ecological Survey.

Dodecaceria capensis Day, 1961: 504.
Type status: Holotype: SAM–A20997.
Type status: Paratype: SAM–A20998.
Locality: 34°11'S 18°39'E, 44 metres (South Africa).
Collected by: UCT Ecological Survey.

Caulleriella Chamberlin, 1919

Caulleriella acicula Day, 1961: 501.
Type status: Holotype: SAM–A20949.
Locality: 33°03,5'S 18°01,5'E, 9 metres.
Type status: Paratype: SAM–A20973.
Locality: 33°04,4'S 17°57,6'E, 30 metres (South Africa)
Collected by: UCT Ecological Survey.

Tharyx Webster & Benedict, 1887

Tharyx filibranchia Day, 1961: 503.
Type status: Holotype: SAM–A21003.
Type status: Paratype: SAM–A21004.
Locality: 34°09,6'S 18°27,4'E, 26 metres (South Africa).
Collected by: UCT Ecological Survey.
Remarks: In Day's unpublished material, *Tharyx filibranchia* is referred to as *Caulleriella filibranchia*.

Cirratulus Lamarck, 1801

Cirratulus gilchristi Day, 1961: 500.
Type status: Holotype: SAM–A20950.
Type status: Paratype: SAM–A20974.
Locality: 33°04,1'S 17°59,7'E, 8–12 metres (South Africa).
Collected by: UCT Ecological Survey.

Cirratulus indicus Day, 1973*a*: 352.
Type status: Paratype: SAM–A21014.
Locality: Ratnagiri, south of Bombay, India.
Collected by: U.D. Gaikwad at Ratnagiri.

Family **Orbiniidae**

Subfamily Protoariciinae

Scoloplella Day, 1963

Scoloplella capensis Day, 1963*a*: 415.
Type status: Paratype: SAM–A20957.
Locality: 33°06,5'S 17°32,9'E, 183 metres (South Africa).
Collected by: UCT Ecological Survey.

Subfamily Orbiniinae

Phylo Kinberg, 1866

Phylo capensis Day, 1961: 476.
Type status: Holotype: SAM–A20908.
Locality: 33°03,6'S 17°56,4'E (South Africa).
Collected by: UCT Ecological Survey.

Scoloplos Blainville, 1828

Scoloplos (*Leodamas*) *uniramus* Day, 1961: 477.
Type status: Syntype: SAM–A21047.
Locality: 34°35'S 21°56'E, 88 metres (South Africa).
Collected by: UCT Ecological Survey.
Remarks: In Day's unpublished material *Scoloplos* (*Leodamas*) *uniramus* is a synonym of *Scoloplos* (*Leodamas*) *johnstonei* Day, 1934.

Scolaricia Eisig, 1914

Scolaricia capensis Day, 1961: 480.
Type status: Holotype: SAM–A20930.
Locality: 34°37'S 21°56'E, 86 metres (South Africa).
Collected by: UCT Ecological Survey.
Remarks: In Day's unpublished material, *Scolaricia capensis* is referred to as *Scoloplos* (*Scoloplos*) *capensis*.

Family **Paraonidae**

Aricidea Webster, 1879

Aricidea suecica simplex Day, 1963*b*: 364.
Type status: Holotype: SAM–A20965.
Locality: 34°25'S 17°36'E, 1 240 metres (South Africa).
Collected by: UCT Ecological Survey.

Aricidea longobranchiata Day, 1961: 482.
Type status: Syntype: SAM–A20968.
Type status: Syntype: SAM–A20964.
Locality: 33°05,5'S 17°53,5'E, 77 metres (South Africa).
Collected by: UCT Ecological Survey.

Aricidea capensis Day, 1961: 481.
Type status: Holotype: SAM–A20963.
Locality: 34°09'S 22°07,1'E, 10 metres (South Africa).
Collected by: UCT Ecological Survey.

Paraonides Cerruti, 1909

Paraonides lyra capensis (Day), 1955: 417 (as *Paraonis lyra* var. *capensis*).
Type status: Syntype: SAM–A20896.
Locality: Knysna Estuary, Cape south coast, South Africa.
Collected by: UCT Ecological Survey.

Family **Opheliidae**

Ophelia Savigny, 1818

Ophelia anomala Day, 1961: 515.
Type status: Paratype: SAM–A20900.
Locality: 34°22,5'S 18°37,3'E, 80 metres (South Africa).
Collected by: UCT Ecological Survey.

Ophelia agulhana Day, 1961: 513.

Type status:	Paratype: SAM–A20899.
Locality:	34°07,1'S 18°35,6'E, 21,7 metres (South Africa).
Collected by:	UCT Ecological Survey.

Family **Scalibregmidae**

Parasclerocheilus Fauvel, 1928

Parasclerocheilus capensis Day, 1961: 517.

Type status:	Holotype: SAM–A20905.
Locality:	Langebaan, Cape west coast, South Africa.
Collected by:	UCT Ecological Survey.

Family **Capitellidae**

Notomastus Sars, 1851

Notomastus fauveli Day, 1955: 422.

Type status:	Paratype: SAM–A20988.
Locality:	Knysna Estuary, Cape south coast, South Africa.
Collected by:	UCT Ecological Survey.

Mediomastus Hartman, 1944

Mediomastus capensis Day, 1961: 518.

Type status:	Holotype: SAM–A20587.
Type status:	Paratype: SAM–A20560.
Type status:	Paratype: SAM–A20589.
Type status:	Paratype: SAM–A20954.
Type status:	Paratype: SAM–A20588.
Locality:	33°04'S 17°59,7'E, 8-12 metres (South Africa).
Collected by:	UCT Ecological Survey.

Family **Maldanidae**

Subfamily Euclymeninae

Euclymene Verrill, 1900

Euclymene natalensis (Day), 1957: 107 (as *Clymene natalensis*).

Type status:	Paratype: SAM–A20976.
Locality:	34°59'S 22°18'E, 105 metres (South Africa).
Collected by:	UCT Ecological Survey.

Euclymene glandularis (Day), 1955: 428 (as *Clymene glandularis*).
Type status: Paratype: SAM–A20975.
Locality: 34°04,47'S 22°13,06'E, 26 metres (South Africa).
Collected by: UCT Ecological Survey.

Macroclymene Verrill, 1900

Macroclymene saldanha (Day), 1955: 428 (as *Clymene* (*Praxillella*) *saldanha*).
Type status: Paratype: SAM–A20943.
Locality: Langebaan, Cape west coast, South Africa.
Collected by: UCT Ecological Survey.

Maldanella McIntosh, 1885

Maldanella capensis Day, 1961: 523.
Type status: Paratype: SAM–A20898.
Locality: 32°15,2'S 28°57,7'E, 47 metres (South Africa).
Collected by: UCT Ecological Survey.

Subfamily Maldaninae

Asychis Kinberg, 1867

Asychis capensis Day, 1961: 521.
Type status: Holotype: SAM–A20966.
Type status: Paratype: SAM–A20967.
Locality: 33°03,5'S 17°58,5'E, 25,5 metres (South Africa).
Collected by: UCT Ecological Survey.

Subfamily Nicomachinae

Nicomache Malmgren, 1866

Nicomache mossambica Day, 1951: 52.
Type status: Syntype: SAM–A20986.
Locality: Inhaca Island, Delagoa Bay, Mozambique.
Collected by: UCT Ecological Survey.

Subfamily Lumbriclymeninae

Clymenura Verrill,1900

Clymenura tenuis (Day), 1957: 110 (as *Leiochone tenuis*).
Type status: Syntype: SAM–A20962.
Locality: Durban Bay, South Africa.
Collected by: UCT Ecological Survey.

Family **Flabelligeridae**

Brada Stimpson, 1854

Brada villosa var *capensis* Day, 1961: 510.
Type status: Holotype: SAM–A20971.
Type status: Paratype: SAM–A20972.
Locality: 34°46'S 22°05'E, 95 metres (South Africa).
Collected by: UCT Ecological Survey.

Pherusa Oken, 1807

Pherusa saldanha Day, 1961: 508.
Type status: Holotype: SAM–A20907.
Locality: 33°03'S 18°00,9'E, 15 metres (South Africa).
Collected by: UCT Ecological Survey.

Diplocirrus Haase, 1915

Diplocirrus capensis Day, 1961: 509.
Type status: Holotype: SAM–A20994.
Type status: Paratype: SAM–A20995.
Locality: 34°15'S 25°0,5'E, 11 metres (South Africa).
Collected by: UCT Ecological Survey.

Family **Sabellariidae**

Sabellaria Savigny, 1817

Sabellaria simplex Day, 1973*a*: 355.
Type status: Syntype: SAM–A21013.
Locality: Ratnagiri, south of Bombay, India.
Collected by: U.D. Gaikwad.

Family **Pectinariidae**

Pectinaria Savigny, 1818

Pectinaria (*Lagis*) *korreni cirrata* Day, 1963*a*: 434.
Type status: Paratype: SAM–A20895.
Locality: 29°53,5'S 31°06,5'E, 71 metres (South Africa).
Collected by: UCT Ecological Survey.

Family **Ampharetidae**

Subfamily Ampharetinae

Ampharete Malmgren, 1866

Ampharete agulhasensis (Day) 1961: 529 (as *Lysippe agulhasensis*).
Type status: Holotype: SAM–A20945.
Type status: Paratype: SAM A20946.
Locality: 34°46'S 22°05'E, 95 metres (South Africa).
Collected by: UCT Ecological Survey.

Ampharete capensis (Day) 1961: 530 (as *Lysippe capensis*).
Type status: Holotype: SAM–A20947.
Type status: Paratype: SAM–A20948.
Locality: 33°02,8'S 18°01'E, 13 metres (South Africa).
Collected by: UCT Ecological Survey

Sabellides Milne-Edwards, 1838

Sabellides capensis Day, 1961: 528.
Type status: Holotype: SAM–A20927.
Type status: Paratype: SAM–A20948.
Locality: 34°11'S 18°01,2'E, 27 metres (South Africa).
Collected by: UCT Ecological Survey.

Samythella Verrill, 1873

Samythella affinis Day, 1963*a*: 435.
Type status: Syntype: SAM–A20956.
Locality: 34°51'S 23°41'E, 183 metres (South Africa).
Collected by: UCT Ecological Survey.

Family **Terebellidae**

Subfamily Thelepinae

Streblosoma Sars, 1872

Streblosoma abranchiata Day, 1963*b*: 369.
Type status: Syntype: SAM–A19770.
Locality: 33°26'S 16°33'E, 2 269 metres (South Africa).
Collected by: UCT Ecological Survey (R. S. *Africana* II).

Telothelepus Day, 1955

Telothelepus capensis Day, 1955: 440.
Type status: Holotype: SAM–A20938.
Type status: Paratype: SAM–A20939.
Locality: Langebaan, Cape west coast, South Africa.
Collected by: UCT Ecological Survey.

Remarks: Although computer records at BM(NH) indicate that the specimens are in their collections, they are in fact held at the South African Museum.

Subfamily Terebellinae

Pista Malmgren, 1866

Pista qolora Day, 1955: 436.
Type status: Paratype: SAM–A20891.
Locality: Qolora shore, East London, South Africa.
Collected by: UCT Ecological Survey.

Remarks: In Day (1967: 740), *Pista qolora* is a synonym of *Pista quadrilobata* (Augener, 1918). In Day's unpublished material, *P. qolora* is a synonym of *P. cetrata* (Ehlers, 1887).

Pista unibranchia Day,1963*a*: 439.
Type status: Paratype: SAM–A20892.
Locality: 34°16,8'S 18°42,8'E, 60 metres (South Africa).
Collected by: UCT Ecological Survey.

Amphitrite Muller, 1771

Amphitrite pauciseta Day, 1963*a*: 439.
Type status: Paratype: SAM–A20959.
Locality: 33°06,4'S 17°44,9'E, 146 metres (South Africa).
Collected by: UCT Ecological Survey.

Family **Sabellidae**

Subfamily Sabellinae

Hypsicomus Grube, 1870

Hypsicomus capensis Day, 1961: 537.
Type status: Holotype: SAM–A20923.
Locality: 34°20'S 24°40'E, 102 metres (South Africa).
Collected by: UCT Ecological Survey.

Potamilla Malmgren, 1866

Potamilla linguicollaris Day, 1961: 539.
Type status: Holotype: SAM–A20906.
Locality: 34°24'S 21°46'E, 18 metres (South Africa).
Collected by: UCT Ecological Survey.
Remarks: In Day's unpublished material, *Potamilla linguicollaris* is referred to as *Perkinsiana linguicollaris*.

Euchone Malmgren, 1866

Euchone capensis Day, 1961: 540.
Type status: Holotype: SAM–A20915.
Type status: Paratype: SAM–A20916.
Locality: 32°06'S 16°37'E, 311 metres (South Africa).
Collected by: UCT Ecological Survey.

Subfamily Fabriciinae

Fabricia Blainville, 1828

Fabricia bansei Day, 1961: 543.
Type status: Holotype: SAM–A20951.
Type status: Paratype: SAM–A20920.
Locality: Mouille Point, Cape Town, South Africa.
Collected by: UCT Ecological Survey.

Fabricia filamentosa Day, 1963*a*: 439.
Type status: Paratype: SAM–A20977.
Locality: 32°08'S 17°39'E, 172 metres (South Africa).
Collected by: UCT Ecological Survey.

Family **Serpulidae**

Subfamily Serpulinae

Pomatoceros Philippi,1844

Pomatoceros americanus Day, 1973*b*: 171.
Type status: Paratype: SAM–A21023.
Locality: Off Beaufort, North Carolina, U.S.A.
Collected by: Duke University Marine Laboratory in Beaufort, N.C., U.S.A.

Ficopomatus Southern, 1921

Ficopomatus capensis Day, 1961: 552.

Type status: Holotype: SAM–A20901.

Locality: 34°24'S 21°46'E, 18 metres (South Africa).

Collected by: UCT Ecological Survey.

Remarks: In Day's unpublished material, *Ficopomatus capensis* is referred to as *Ovopomatus capensis*.

Neovermilia Day, 1961

Neovermilia capensis Day, 1961: 551.

Type status: Holotype: SAM–A20935.

Locality: 34°23,3'S 18°39,4'E, 97 metres (South Africa).

Collected by: UCT Ecological Survey.

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NEAR-BOTTOM AND PELAGIC GAMMARIDEAN AMPHIPODS IN THE WESTERN INDIAN OCEAN

by

GEORGYI M. VINOGRADOV

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NEAR-BOTTOM AND PELAGIC GAMMARIDEAN AMPHIPODS IN THE WESTERN INDIAN OCEAN

by

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With 10 figs and 2 tables

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ABSTRACT

Between October 1988 and February 1989, a collection of pelagic and benthopelagic gammarids was taken during the seventeenth cruise of R/V *Vityaz* in the tropical (Seamount Error, Mozambique Channel and Saya de Malha Bank) and subtropical (Walters Shoal) regions of the Western Indian Ocean. A total of 2 362 specimens of 34 gammaridean species were found, four of which (*Amaryllis maculata*, *Scopelocheiropsis sublitoralis*, *Ichnopus walkeri* and *Regalia oculata*) are described as new to science. Comparison of the near-bottom and pelagic samples permitted detection of a group of animals mainly confined to the near-bottom water. A key to lysianassoid amphipods of the genus *Trischizostoma* is given.

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INTRODUCTION

Amphipods form an important element of marine pelagic communities. They inhabit the surface and deep waters of the ocean at all latitudes from the equator to the polar areas. They do not usually form dense populations, but their diversity and the diversity of their life-forms can be high. All amphipods are of benthic origin, but representatives of their different suborders have radiated into pelagic biotopes to differing extents. Unlike the hyperiids, which have become completely pelagic, and the caprellids and ingolphyellids, which have practically no pelagic representatives, some Gammaridea have penetrated into this biotope.

The overwhelming majority of marine gammarids are benthic epifaunal species. However, only a few benthic gammarideans (mainly inhabitants of secluded biotopes, e.g. wood-borers, some symbionts of benthic animals or highly specialized phytal animals) never leave the sea floor. The majority of benthic gammarideans, representing the most diverse life-forms, enter the pelagial some way or other. All stages of expansion into pelagic waters may be traced among them. Some may rise briefly into the near-bottom layer, some make regular migrations into the meroplankton, others may have a long pelagic life without losing all connection with the bottom and, ultimately there are those with a purely pelagic way of life (Vinogradov 1992, 1995). Less than 4 per cent of marine gammaridean species are in this final category: about 100 species of 50 genera, almost all of them belonging to families which also have benthic representatives.

Usually it is the purely pelagic gammarideans that are captured by samplers operating at a considerable distance from the bottom. Other gammarideans from the near-bottom layers are difficult to catch and therefore are poorly represented in collections. It is clearly necessary to carry out near-bottom trawlings as well as pelagic ones in order to obtain a complete picture of a pelagic gammaridean's taxocene. However, near-bottom trawling is fraught with considerable technical difficulties, and consequently the ocean's near-bottom layers have been studied to a considerably lesser extent than purely pelagic or benthic communities. This is certainly true of the Indian Ocean, where the purely pelagic gammaridean fauna has been investigated in detail by past expeditions (of the R/V *Dana*, *Siboga*, *Vityaz* (old)[1] and others). The near-bottom fauna is known to a much lesser extent.

In 1974, during the seventeenth cruise of the Russian R/V *Akademik Kurchatov* to Peruvian coasts, hauls in the near-bottom layer were successfully carried out for the first time using an Isaacs-Kidd midwater trawl with a pressure vibration transducer, the signal of which was transmitted through the cable rope to the frequency meter mounted on the vessel. The transducer reading permitted continuous information on the precise depth of the trawl, and simultaneous measurement of bottom depth with the echosounder permitted deployment of the trawl in the immediate proximity of the bottom. In 1987 this method was used extensively during the eighteenth cruise of R/V *Professor Stockman* to the

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[1] 'Old' *Vityaz,* historically the third Russian research vessel bearing this name, operated between 1949 and 1979. Expeditions of the 'new' *Vityaz* (sometimes incorrectly mentioned in articles as *Vityaz-IV* or *Vityaz-II*) began in 1981.

Pacific submerged ridges, Nazka and Sala-y-Gomez (Rudjakov & Zaikin 1990). That cruise, in particular, gathered a great deal of near-bottom gammaridean material from this region (Vinogradov 1990*b*).

MATERIALS AND METHODS

Between October 1988 and February 1989, analogous works were carried out during the seventeenth cruise of R/V *Vityaz* (new) in the tropical (Seamount Error Mountain (EM), Mozambique Channel (MC) and Saya de Malha Bank (SdM)) and subtropical (Walters Shoal (W)) regions of the Western Indian Ocean[2]. The specimens of pelagic and benthopelagic gammarideans collected by this expedition are the basis of the present work.

Animals were collected with the following apparatus:

1. Samyshev-Aseev modification of the Isaacs-Kidd midwater trawl (IKSAMT) with transducer (see above). Trawl mouth area was 5.5 m^2, the net was 25 m long and made completely out of 5 mm mesh, a sieve frame (1.3 mm mesh, 5 m length) was fitted at the cod-end. Two types of haul were performed: near-bottom trawling at distances of 10–30 m from the bottom (NBT) and pelagic trawling far from the bottom (PT). In all, 28 hauls were carried out in tropical regions and 24 on the Walters Shoal, yielding 1 788 and 502 gammarideans, respectively.

2. Towed underwater apparatus 'Sound', or 'Zvuk' in the Russian language (TUA 'Sound') (Biryukov *et al.* 1990). For plankton studies the construction of the apparatus was modified by the addition of a sampler consisting of two nets with mouth area 0.12 m^2 and mesh size 0.178 mm. The nets were opened and closed successively using the Tucker principle. Control signals for operation of the release gear are applied autonomously at each of the locks. Constancy of distance from the bottom was maintained by the winch operator using TV images during tows near the bottom, and by the apparatus' own echo-sounder in other cases. Hauls of 30 to 60 minutes duration were made at distances of 2 m and 30 m from the bottom (mfb) at each station. In all, 35 stations were sampled with the TUA (15 on the Walters Shoal) from which 61 gammarideans were taken (Note: a preliminary list of these species was published by Vinogradov (1990*a*). Here it is made more precise and given in the final variant (Table 1)).

3. Big Juday plankton net (BDN 37/50) with mouth area 0.1 m^2 and mesh size 0.18 mm

4. Oceanic model of Juday plankton net (ODN 80/113) with mouth area 0.5 m^2 and mesh size 0.18 mm.

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[2] One can find detailed descriptions of the Walters Shoal and zoogeographical analysis of its position in Collete & Parin (1991).

Standard catching layers during stations with the Juday nets were 1 000–500, 500–250, 250–100, 100–50 and 50–0 m from the surface. If ocean depth at the point was less than 1 000 m, the lower limit of the deepest haul was selected at a distance of 50 m from the bottom. The Juday net hauls were usually accompanied by hauls with the TUA 'Sound'. In this case 'Sound' works received the next station number (for example, st. 2648–ODN and st. 2649–TUA), but catches were carried out in the same point. Only 11 gammarideans were taken in all catches by both models of the Juday nets.

Detailed information on the hauls yielding gammarideans is given in Station List (Tables A–D, pages 80 to 83). All the gammarideans captured are considered below[3], together with data on the sampling gear, station number, region, time of capture (D = day; N = night), depth and characteristics of the haul (NBT-PT for IKSAMT, n mfb for TUA 'Sound').

TABLE 1

Gammaridean abundances at different distances above the sea bed (on basis of hauls of TUA 'Sound' and Juday nets, number of individuals)

Group	Species	TUA 'Sound' 2 mfb	30 mfb	Juday nets (near-bottom hauls)
Pelagic	*Cyphocaris anonyx*	5	3	–
	C. challengeri	–	2	1
	Stenopleura atlantica	–	1	1
	**Eusirella ?elegans* juv.	–	2	–
	**Stenopleuroides macrops*	18	4	–
	**Halice macronyx*	–	1	–
	Bathystegocephalus globosus	–	1	1
	Parandania boecki	1	–	–
Benthopelagic	**Orchomene pelagica*	1	–	–
	**Eurythenes gryllus* juv.	–	1	–
	**Ichnopus walkeri* sp. nov.	3	–	–
	**Scopelocheiropsis sublitoralis* sp. nov.	2	–	–
	**Parargissa curticornis*	–	1	–
	**Ampelisca brevicornis*	1	–	–
	**Stegocephaloides attingens*	5	–	2
	*?*Eusirus crosnieri* (damaged spcm.)	2	1	–
	**Paramoera austrina*	1	–	–
	**Halicoides tambiella*	2	2	–
	**Halicoides discoveryi*	–	1	1

NB: asterisk (*) indicates amphipods which were found only in the near-bottom hauls (in all material).

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[3] For a description of the collection of hyperiidean amphipods taken by these catches from the Walters Shoal see G. Vinogradov (1993).

DESCRIPTION OF MATERIAL

KEY TO ABBREVIATIONS IN FIGURES

AI–AII – antennae I and II; **L** – lower lip; **Md** – mandible; **MxI–MxII** – maxillae I and II; **Mxp** – maxilliped; **PI–PVII** – pereopods I–VII (pereopods I and II = gnathopods I and II); **EpIII** – epimeron III; **UI–UIII** – uropods I–III; **T** – telson.

LIST OF SPECIES

Lysianassoidae
Trischizostoma barnardi
Trischizostoma tanjae
Amaryllis maculata sp. nov.
Erikus dahli
Cyphocaris anonyx
Cyphocaris challengeri
Cyphocaris richardi
Cyphocaris faurei
Cyphocaris cornuta
Paracyphocaris praedator
Scopelocheiropsis sublitoralis sp. nov.
Eurythenes gryllus
Eurythenes obesus
Ichnopus pelagicus
Ichnopus walkeri sp. nov.
Thoriella islandica
Orchomenella pelagica

Hyperiopsidae
Parargissa curticornis

Stegocephalidae
Parandania boecki
Bathystegocephalus globosus
Stegocephaloides attingens

Pardaliscidae
Halice tenella
Halice macronyx
Halicoides discoveryi
Halicoides tambiella

Ampeliscidae
Ampelisca brevicornis

Synopiidae
Synopia variabilis

Eusiridae
Eusirus crosnieri
Eusiropsis riisei
Eusirella ?elegans
Stenopleura atlantica
Stenopleuroides macrops
Regalia oculata sp. nov.
Paramoera austrina

Superfamily LYSIANASSOIDAE
(= Family **Lysianassidae** s.l.)

Trischizostoma Boeck, 1861

The species belonging to this genus are semiparasitic. They have strong prehensile pereopods and narrow piercing mouthparts. The genus falls into two distinct groups. The first group includes *T. serratum*, *T. remipes* and *T. paucispinosum*, characterized by telson cleft to middle and weakly specialized mouthparts. They are symbionts of benthic animals, e.g. sponges (K. Barnard 1925). Representatives of the second group rise up into the water column where they occupy an atypical ecological niche for gammaridean amphipods. They are ectoparasites of fishes, mainly of sharks (Stephensen 1935; Vader & Romppainen 1985). These species have telson small entire (only one—*T. crosnieri*—weakly cleft) and highly specialized mouthparts, e.g. maxillae are elongated stylets, mandibles are narrow and have well-developed incisors, maxillipeds are considerably reduced, and they have digitate grooved inner plates.

It is a long time since the existing key to *Trischizostoma* was published in English[4] (J.L. Barnard 1961) and the genus now includes more than twice the number of species as it did then (see Ledoyer 1978; G. Vinogradov 1990*b*, 1991; Lowry & Stoddart 1993, 1994). A new key that includes all the *Trischizostoma* species known to 1996 is provided.

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[4] Russian key to the genus *Trischizostoma* was published by Vinogradov (1991) and does not include recently described *T. crosnieri* and *T. richeri* (see Lowry & Stoddart 1993, 1994).

Trischizostoma barnardi G. Vinogradov, 1990

Trischizostoma barnardi G. Vinogradov, 1990*b*: 37.

Material

IKSAMT: st. 2598 (MC), D, PT 400 m—1 specimen, 7 mm.

Distribution

Formerly recorded from the Pacific Ocean (submerged Nazka Ridge).

Trischizostoma tanjae G. Vinogradov, 1991

Trischizostoma tanjae G. Vinogradov, 1991: 26.

Material

IKSAMT: st. 2575 (EM), D, NBT 380–400 m—5 ♂, 5–7.5 mm; st. 2576 (EM), D, PT 50–0 m—1 ♀, 6 mm; st. 2823 (EM), D, NBT 390–400 m—139 specimens, 5–7 mm; st. 2826 (EM), N, NBT 390–370 m—3 ♀, 7.5–8 mm, 1 ♂, 7.5 mm, 7 juv., 5–7 mm.

Description

The description of *T. tanjae* published elsewhere was based on this collection, all specimens of which must be regarded as type material. The holotype (♀ reif. 5 mm, from st. 2575) and most of the paratypes are stored in the Zoological Museum of the Moscow State University, Moscow (ZMMU), holotype No Mb–032 and paratypes No Mb–1013 (104 specimens) and Mb–1033. However, 25 paratypes from st. 2823 have been deposited in the South African Museum (catalogue numbers SAM–A40854 to SAM–A40878).

Distribution

Found only near the submerged Error Mountain (Indian Ocean).

Remarks

Sharks, as has already been noted, are the typical hosts of fish-associated semiparasitic *Trischizostoma*. On the Error Mountain, near-bottom catches of commercial fish and shrimp trawls included numerous sharks *Halaelurus hispindus* (Scyliorhinidae). Sharks made up 12 per cent of the total number of caught fishes (Scherbatchev 1989). *Halaelurus hispindus* may be a host of *T. tanjae*. During the *Vityaz* cruise, many *H. hispindus* were caught near the Socotra Island, but unfortunately no IKSAMT trawling was done there to catch amphipods. In other regions, neither *H. hispindus* nor *T. tanjae* were found.

KEY TO THE GENUS *TRISCHIZOSTOMA*

1A. Telson partly cleft 2
1B. Telson entire 5

2A. Pereopod I dactyl inner margin serrate .... *T. serratum*
2B. Pereopod I dactyl inner margin smooth 3

3A. Palm of pereopod I very spinose 4
3B. Palm of pereopod I scarcely spinose .... *T. pincispinosum*

4A. 6th article of pereopod I 1.5 times as wide as long. 7th article of pereopod VII slender (normal dactyl).. *T. crosnieri*

4B. 6th article of pereopod I 2–3 times as wide as long. 7th article of pereopod VII oval .... *T. remipes*

5A. Maxillipedal palp much longer than outer plates of maxillipeds 6
5B. Maxillipedal palp not longer than outer plates of maxillipeds 12

6A. Pereopod I 6th article oval, width exceeding length by at least 1.5 times 7
6B. Pereopod I 6th article of another shape. Width never exceeding length by more than 1.5 times. If length:width ratio approximates to 1.5, the posterior margin of 6th article forms a distinct angle with palmar margin so that article is nearly triangular 10

7A. Pereopod I 6th article spiniferous palmar margin without triangular processes 8
7B. Pereopod I 6th article spiniferous palmar margin with triangular processes .... *T. denticulatum*[5]

8A. Pereopod II 5th article as long as or slightly longer than 3rd article and twice as long as oval 6th article. Pereopod III 2nd article twice as long as 5th article. Pereopod VI 2nd article as long as 4th and 5th articles combined 9
8B. Pereopod II 5th article shorter than 3rd article and not more than 1.5 times as long as pyriform 6th article. Pereopod III 2nd article not longer than 5th article. Pereopod VI 2nd article shorter than 4th and 5th articles combined .... *T. macrochela*[6]

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[5] Ledoyer (1978) did not find eyes in *T. denticulatum* but suggested that they may have disappeared as a result of preservation of the specimen. So this character is not included in this key.

[6] The description of *T. macrochela* erroneously reported that the palp of maxilla I is completely absent (Vinogradov 1990*b*). Repeated investigation of the holotype shows that a very delicate 1-articulated rudimentary palp of maxilla I (without any setae) is present in *T. macrochela*.

9A. Rostrum length greater than half head. Pereopod VI 2nd article length hardly exceeds its width .... *T. longirostra*
9B. Rostrum length does not exceed half of head. Pereopod VI 2nd article length clearly exceeds its width .... *T. richeri*

10A. Coxa II maximum height equal to that of the corresponding pereonite. Rostrum horizontal, its top reaching beyond peduncle of antenna I 11
10B. Coxa II maximum height equal to half height of corresponding pereonite. Rostrum rounded, its top not reaching beyond peduncle of antenna I ... *T. nicaeense*

11A. Coxae II to VII decreasing in height progressively. Pereopod I 6th article approximately triangular, with pronounced angle between palmar and posterior margins .... *T. rashii*

11B. Coxae II to IV equally high. Coxa V half as high as coxa IV. Other coxae decreasing in height progressively. Pereopod I 6th article irregularly rounded .... *T. circulare*

12A. Maxillipedal palp half as long as outer plates of maxillipeds. Pereopod I 6th article spiniferous palmar margin is even. Pereopods V to VII 2nd articles posterior margins rounded lobate .... *T. nascaensis*
12B. Maxillipedal palp is slightly shorter than outer plates of maxillipeds. Pereopod I 6th article spiniferous palmar margin forming declivitous serrations or pronounced outgrowth. At least pereopod VII 2nd article posterior margin is concave or skewed distally 13

13A. Pereopod II 6th article length exceeds width. Maxillipedal palp with all 3 articles approximately equal in length 14
13B. Pereopod II 6th article width exceeds length. Maxillipedal palp 2nd article twice as long as first or third .... *T. tanjae*

14A. Pereopod I 6th article spiniferous palmar margin with declivitous serrations. Pereopod V 2nd article posterodistal margin skewed. Uropod III rami half as long as peduncle .... *T. barnardi*
14B. Pereopod I 6th article spiniferous palmar margin with a ridge of large outgrowths. Pereopod V 2nd article posterodistal margin forming a round lobe. Uropod III rami slightly longer than peduncle .... *T. cristochelata*

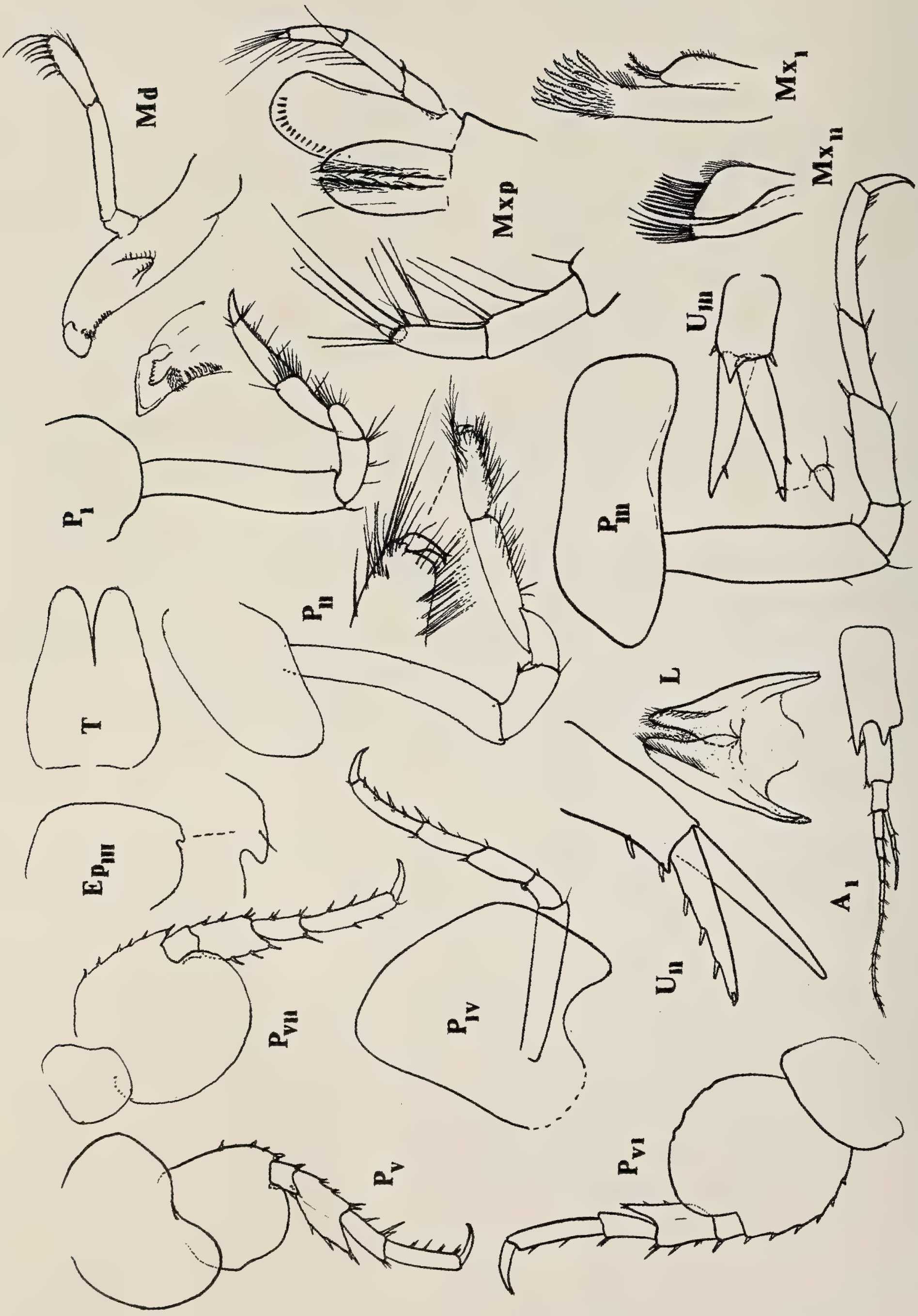

Figure 1
Amaryllis maculata sp. nov. Holotype.

Amaryllis Haswell, 1880

Amaryllis maculata sp. nov.
Fig. 1

Material

IKSAMT: st. 2725 (W), N, NBT 20 m—1 ♀ juv., 6.5 mm (holotype, SAM–A40879).

Type locality

Walters Shoal.

Description

Juvenile female 6.5 mm long. Body smooth, without thorns and carina. Urosome segment I with dorsal depression. Eyes large, black, kidney-shaped.

Antennae I and II in living specimens with red rings around the distal parts of all articles, pereonal, pleonal and urosomal segments also with red bands on posterior margin, centre of coxae IV and V and pereopods VI and VII basal articles each with red spot.

Lateral cephalic lobe large, quadriform, rounded. Rostrum short, blunt, recurved. Antenna I with peduncle articles cylindrical; 1st peduncle article twice as long and broad as 2nd, 2nd twice as long and broader than 3rd, flagellum 12-articulate, accessory flagellum 5-articulate. Antenna II subequal to antenna I.

Lower lip lacking inner lobes and with narrow mandibular processes.

Mandible, incisor smooth, spine row well developed, molar weak, conical; palp attached slightly proximal to molar, palp second article linear, 1.5 times as long as article 3. Maxilla I lacking palp; outer plate narrow, linear, longer than inner, with 11 serrate teeth distally, medial margin with fine setae distally, inner plate with 2 pinnate setae distally, medial margin setulose. Maxilla II inner and outer plates subequal, outer plate narrower than inner, both having long, strong spine-setae distally.

Maxilliped inner plate well developed, narrow, reaching ⅔ along outer; outer plate elongate with distomedial row of small submarginal spines, palp slightly exceeding outer plate, bearing few weak long setae, 4th article rudimentary, bearing two long apical setae.

Pereopod I simple, short, second article linear, slightly bent, as long as articles 4–7 combined; article 6 slightly longer than article 5. Pereopod II subchelate, 2nd article linear, shorter than articles 4–6 combined, 5th article sublinear, about 1.5 times as long as 6th; palm short, not lunate, sub-straight, dactyl short and covering 100 per cent of palmar edge.

Coxa III and IV much deeper than II; coxa IV substantially excavate posteriorly with posteroventral lobe somewhat round, pointed dorsally. Pereopods III and IV subequal, 2nd article linear, equal to 5th and 6th articles combined, 4th subequal to 5th but broader; 6th article linear, slightly curved, 1.2–1.5 times as long as 5th. Coxae V–VII height decreasing from V to VII. Coxa V with weak posterior lobe. Pereopod V shorter than subequal VI and VII. Pereopods V–VII article 2 with well developed rounded posteroventral lobe; article 4 expanded posteriorly and bearing few spines along anterior and posterior margins; pereopods V–VII article 6 linear, longer and slightly narrower than article 5; dactyl strong and slightly curved.

Epimeron III weakly extended posteriorly with small sinus posteroventrally.

Uropod I peduncle with lateral row of spines; uropod II inner ramus shorter than outer ramus, bearing row of spines; uropod III aequiramous, ordinary, peduncle short with apicomedial tooth, outer ramus 2-articulate.

Telson cleft 50 per cent of length, width 70 per cent of length, lateral margins slightly excavate, narrowly gaping with apically rounded lobes.

Remarks

Many details of the morphology of *A. maculata* sp. nov., i.e. form of the eyes and rostrum, mandibular palp, form and proportions of pereopod articles, resemble those of *A. macrophthalma*. However, *A. maculata* has maxilliped outer plates of another form, maxilla II with broad inner plate, telson with concave edges and some other characters, which clearly separate it from *A. macrophthalma*.

Neither our specimen of *A. maculata* sp. nov., nor J. Barnard's specimen of *A. macrophthalma* (see Barnard 1972), have the inner edge of uropod II inner ramus incised. Such an incision is shown for *A. macrophthalma* by Stebbing (1888) and is found on other species of the genus and in closely related genera (*Erikus*, for example), though it is not shown by *Bathyamaryllis* (see Pirlot 1933). This incision is also absent in the new species of this lysianassoid group described from the Red Sea. It constituted the main reason for the description of the genus *Pseudoamaryllis* by Andres (1981). But, as can be seen, this character is not reliable, so the validity of *Pseudoamaryllis* may be doubtful.

Biotope

This individual was caught on the top of Walters Shoal. Based on the results of Sigsbee trawlings, diving and TV observations, the top was covered by stones with narrow gaps between them, covered by thalloid red algae and encrusted by dominant calcareous coralline algae *Mesophyllum syrphetodes*—see Collet & Parin (1991). This article includes a photograph of the bottom at st. 2691 of the R/V *Vityaz*, taken at practically the same position as st. 2725 (Collet & Parin 1991, fig. 2).

Erikus Lowry & Stoddart, 1987

Erikus dahli Lowry & Stoddart, 1987
Fig. 2.

Erikus dahli Lowry & Stoddart, 1987: 1304.

Material

IKSAMT: st. 2799 (SdM), N, NBT 300–220 m—3 ♂, 6–6.5 mm (SAM–A40880).

Distribution

Temperate water near the Chile coast. Lowry & Stoddart (1987) assumed that some species of this genus were found near South Africa. A new record from Saya de Malha Bank broadens the known distribution of this species.

Remarks

Our specimens correspond to the description and figures of typical specimens. However, our animals are noticeably smaller than the holotype (21.4 mm) and one of the paratypes (13 mm), although other paratypes have lengths between 6 and 7 mm, similar to our specimens.

Cyphocaris Boeck, 1871

Cyphocaris anonyx Boeck, 1871

Cyphocaris anonyx Boeck, 1871: 104; 1872: 141. Schellenberg, 1926*a*: 210. Birstein & Vinogradov, 1955: 212. *Non* Chilton, 1912: 464.

Cyphocaris micronyx Stebbing, 1888: 656. Chevreux, 1900: 165.

Material

IKSAMT: st. 2575 (EM), D, PT 380–400 m—4 specimens, 8.5–10.5 mm; st. 2597 (MC), N, NBT 360–550 m—1 specimen, 6.5 mm; st. 2604 (MC), N, NBT 680 m—8 specimens, 4–12 mm; st. 2642 (MC), N, PT 1200 m—1 specimen, 10.5 mm; st. 2714 (W), D, NBT 1 000 m—8 specimens, 8.5–11 mm; st. 2717 (W), N, PT 1 000 m—6 specimens, 9.5–12.5 mm; st. 2720 (W), D, PT 850–730 m—8 specimens, 8–12 mm; st. 2799 (W), D, PT 620–600 m—6 specimens, up to 12 mm; st. 2773 (W), N, PT 1 150 m—6 specimens, up to 13 mm; st. 2788 (SdM), N, PT 400 m—1 specimen, 10 mm; st. 2789 (SdM), N, PT 1 000 m—10 specimens, 11.5–13 mm. **TUA 'Sound'**: st. 2661 (MC), D, 300–260 m (2 mfb)—4 juv., 3 mm each; st. 2678 (W), N, 840–820 m (2 mfb)—1 damaged specimen; st. 2681 (W), N, 450–480–310 m (30 mfb)—1 damaged specimen; st. 2737 (W), D, 1 085–1 090 m (30 mfb)—1 specimen, 6 mm and 1 exuviae; st. 2798 (SdM), N, 230–255 m (30 mfb)—1 juv. specimen.

Distribution

Cosmopolitan, meso- and bathypelagic.

Cyphocaris challengeri Stebbing, 1888

Cyphocaris challengeri Stebbing, 1888: 661; 1906: 29. Schellenberg, 1926*a*: 243. G. Vinogradov, 1990*b*: 40.

Cyphocaris alicei Chevreux, 1905*b*: 1. Walker, 1909: 327. *Non* Strauss, 1909: 67.

Cyphocaris kincaidi Thorsteinson, 1941: 58.

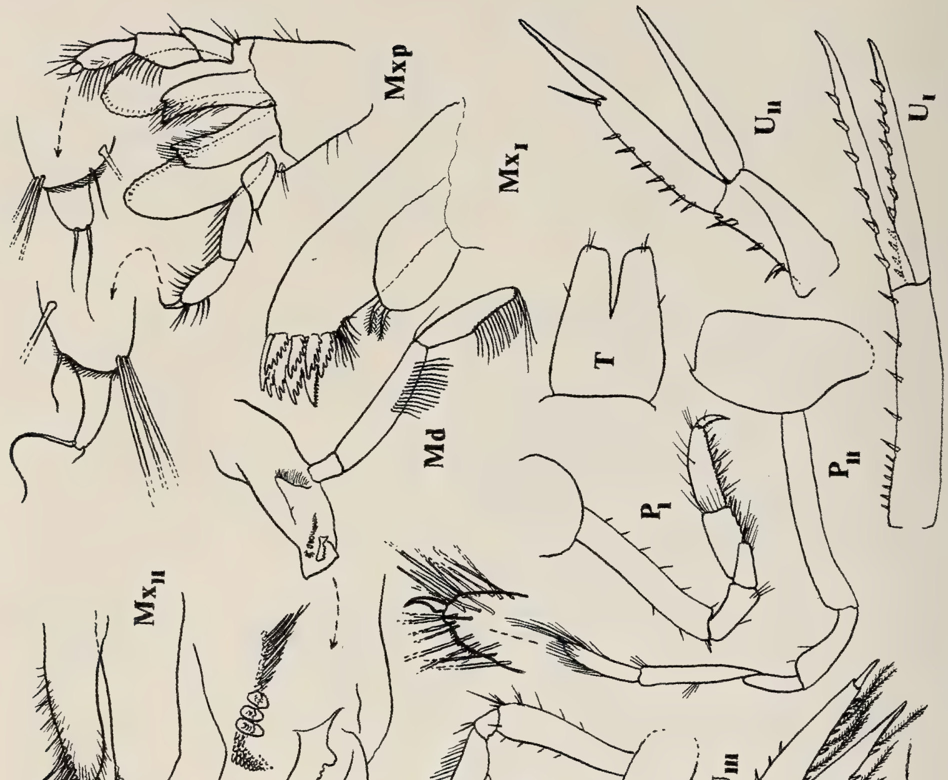

Figure 2
Erikus dahli. Male, length 6.5 mm. St. 2799.

Material

IKSAMT: st. 2578 (EM), N, PT 380–400 m—10 specimens, 8–14 mm; st. 2598 (MC), D, PT 400 m—3 specimens, 5.5–8 mm; st. 2605 (MC), D, PT 460–700 m—1 specimen, 10 mm; st. 2675 (W), N, PT 1 000 m—1 specimen, 12 mm; st. 2712 (W), N, PT 100 m—1 specimen, 9 mm; st. 2714 (W), D, NBT 850–650 m—1 specimen, 10.5 mm; st. 2719 (W), N, PT 200 m—1 specimen, 11 mm; st. 2720 (W), D, PT 850–730 m—2 specimens, 10 mm each; st. 2727 (W), N, PT 150 m—1 specimen, 8 mm; st. 2773 (W), N, PT 1 150 m—4 specimens, up to 13 mm; st. 2776 (W), N, PT 200 m—5 specimens, up to 9 mm; st. 2777 (W), N, PT 200 m—3 specimens, up to 10 mm; st. 2787 (SdM), N, PT 100 m—21 specimens, up to 15 mm; st. 2788 (SdM), N, PT 400 m—10 specimens, up to 13 mm; st. 2789 (SdM), N, PT 1 000 m—10 specimens, 9.5–14.5 mm; st. 2794 (SdM), D, NBT 300–650 m—59 specimens, 7–11 mm; st. 2799 (SdM), N, NBT 300–200 m—9 specimens, 7–10 mm; st. 2800 (SdM), N, PT 200 m—3 specimens, up to 8 mm; st. 2805 (SdM), D, PT 200 m—14 specimens, up to 10 mm; st. 2807 (SdM), N, NBT 200 m—12 specimens, up to 13 mm. **TUA 'Sound'**: st. 2647 (MC), N, 400–470 m (30 mfb)—1 specimen, 4 mm; st. 2655 (MC), N, 1 210—1 215 m (2 mfb)—1 exuviae, 11 mm; st. 2792 (SdM), D, 266 m (30 mfb)—1 juv., 4 mm. **ODN 80/113**: st. 2586 (0°27'N 56°03'E – Equator Mountain), N, 500–250 m—1 ♀, 12 mm, with 49 eggs in marsupium; st. 2656 (MC), N, 1 000–500 m—1 juv., 3 mm.

Distribution

Atlantic, Pacific, Indian and Southern Oceans, mesopelagic.

Cyphocaris richardi Chevreux, 1905

Cyphocaris richardi Chevreux, 1905*a*: 1. Schellenberg, 1926*a*: 245. 1926*b*: 206. Birstein & Vinogradov, 1955: 12.
Cyphocaris anonyx Chilton, 1912: 464 (*non* Boeck, 1871:104).

Material

IKSAMT: st. 2616 (MC), N, PT 1 700–1 900 m—1 specimen, 23 mm; st. 2717 (W), N, PT 1 000 m—1 juv., 13.5 mm; st. 2773 (W), N, PT 1 150 m—7 specimens, up to 12 mm; st. 2789 (SdM), N, PT 1 000 m—1 specimen, 24 mm.

Distribution

Cosmopolitan, abysso- and bathypelagic.

Cyphocaris faurei Barnard, 1916

Cyphocaris faurei K. Barnard, 1916: 117. Schellenberg, 1926*a*: 215. G. Vinogradov, 1990*b*: 41.
Cyphocaris alicei Strauss, 1909: 67 (*non* Chevreux, 1905*b*: 1).

Material

IKSAMT: st. 2604 (MC), N, NBT 680 m—7 specimens, 9–30 mm; st. 2605 (MC), D, PT 460–700 m—3 specimens, 17, 25 and 28 mm; st. 2616 (MC), N, PT 1 700–1 900 m—1 specimen, 29 mm; st. 2789 (SdM), N, PT 1 000 m—1 specimen, 22 mm.

Distribution

Circumoceanic in southern hemisphere, also in the Gulf of California, mesopelagic.

Cyphocaris cornuta Ledoyer, 1978

Cyphocaris cornuta Ledoyer, 1978: 375.

Material

TUA 'Sound': st. 2655 (MC), N, 1 190–1 210 m (30 mfb)—1 exuviae, 10 mm.

Distribution

Mozambique Channel.

Paracyphocaris Chevreux, 1905

Paracyphocaris praedator Chevreux, 1905

Paracyphocaris praedator Chevreux, 1905*c*: 1. Shoemaker, 1945: 189. Bowman & Wasmer, 1984: 844.

Material

IKSAMT: st. 2616 (MC), N, PT 1 700–1 900 m—1 ♂, 8 mm.

Distribution

Cosmopolitan, bathypelagic.

Remarks

Bowman & Wasmer (1984) found three *P. praedator* among the attached eggs of the shrimp *Oplophorus novaezeelandie*. They suggested that *P. praedator* is an egg-mimic that feeds on the *Oplophorus* eggs. The prehensile pereopods of *Paracyphocaris* prevent it from being dislodged by the host's grooming.

Scopelocheiropsis Schellenberg, 1926

Scopelocheiropsis sublitoralis sp. nov.

Fig. 3.

Material

TUA 'Sound': st. 2661 (MC), D, 300–258 m (2 mfb)—1 ♂, 4.5 mm (holotype, SAM–A40881) and 1 juv., 2.5 mm (paratype). Paratype is stored in the P.P. Shirshov Institute of Oceanology of the Russian Academy of Sciences.

Bottom at st. 2661

Mud with sand.

Type locality

Mozambique Channel.

Description

Male, 4.5 mm. Body smooth, without thorns. Urosomit I with low convex carina. Rostrum small. Epistome hangs over upper lip.

Antenna I shorter than II, peduncle articles broad, the length of each article less than breadth, 1st article longer than 2nd and 3rd combined. Flagellum proximal articles fused conical. Distal part of flagellum 8-articulate. Accessory flagellum 3-articulate. 1st article longer than 2nd and 3rd combined. Antenna II peduncle articles broad, subrectangular, margin with few transverse rows of short setae; flagellum 27-articulate.

Lower lip lacking inner lobes, mandibular process narrow.

Mandible, incisor smooth convex, lacinia mobilis well developed, spine row short, molar absent. Palp strong, 2nd article much longer than 3rd, both with a row of long setae distally on medial margin.

Maxilla I inner plate shorter than outer, with row of 10 pinnate setae. Palp well developed, 2nd article expanded distally, apex broad, truncate with 7 apical spines (forked or serrate).

Maxilla II plates subequal, distal margin of both plates having row of long strong setae varying from pinnate to smooth.

Maxilliped well developed, palp 4-articulate, inner plate reaching middle of palp article 1, apex truncate with 4 short rounded spines, present a row of long pinnate setae apicomedially; outer plate oval, nearly reaching distal margin of palp article 3, bearing 3 long pinnate setae apically and row of long spines on medial margin.

Coxae I–IV not densely setose distally. Coxa I trapeziform, expanded distally, anterodistal angle blunt. Pereopod I scopelocheirin in structure, article 2 equal to articles 5 and 6 taken together, 6th longer than 5th, dactyl very vestigial and shrouded in setae. Pereopod II subequal to pereopod I; 5th article drop-like, 6th rounded-oval, 1.5 times longer than wide, dactyl emanating from middle of article 6 apex, palm straight, short, one half of the distal margin, both articles 5 and 6 thickly covered by short and long setae.

Pereopods III and IV stout, 2nd articles dilated distally and equal to 5th and 6th articles

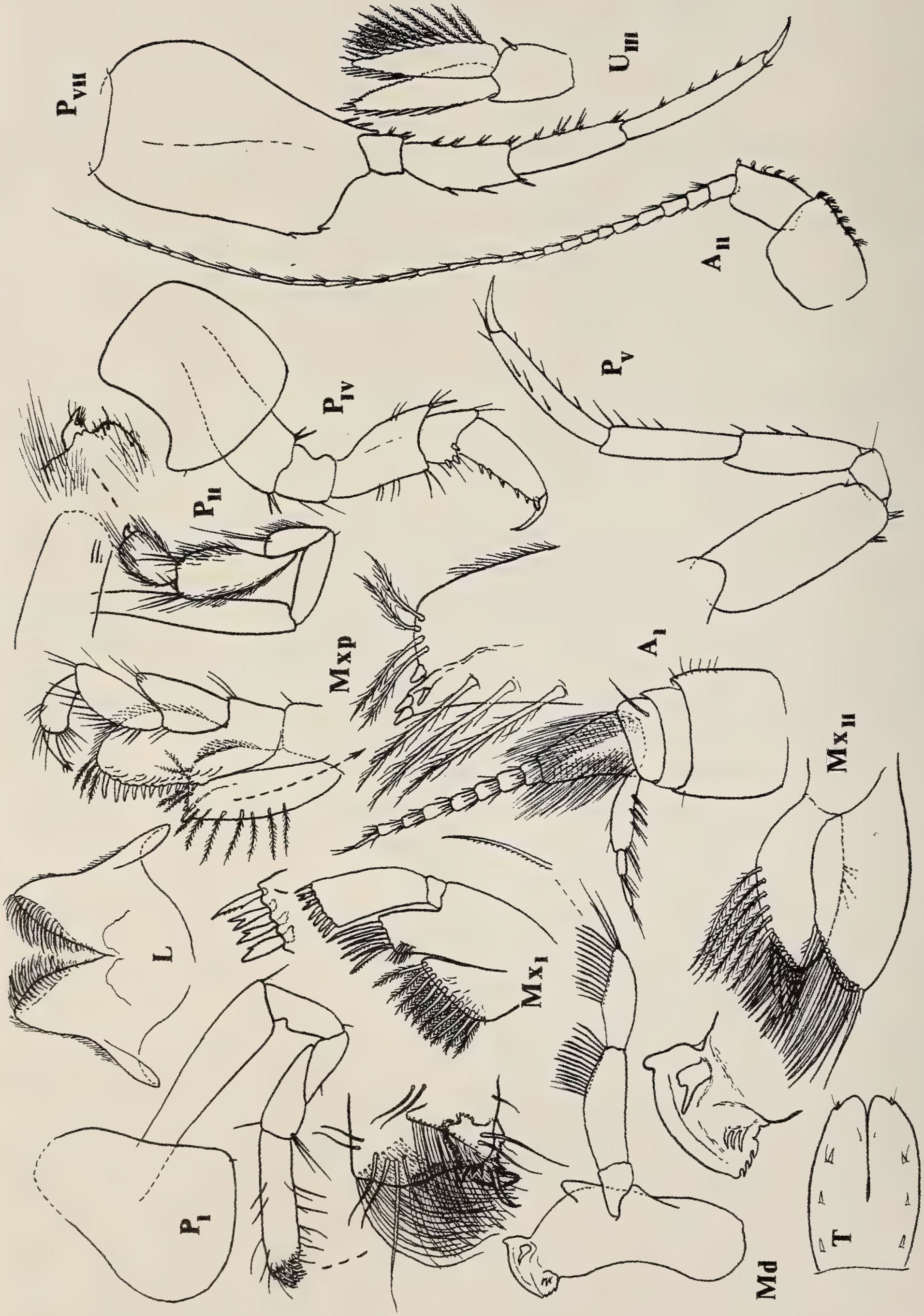

Figure 3
Scopelocheiropsis sublitoralis sp. nov. Holotype.

taken together, 5th article 1.5 times shorter than wide, its posterodistal corner with setae and short spines, 6th article conical, 2.5 times longer than 5th, with short spines on the posterior margin and strong blunt spine at base of dactyl.

Pereopod V slender, 2nd article oblong-oval without distal lobe, dactyl sharp and slightly curved, one quarter as long as 6th article. Pereopod VII 2nd article broad, anterior margin concave distally and convex proximally, posterodistal lobe obliquely blunted distally and not overreaching 3rd article, 4th and 5th articles subequal, 6th rather slender and longer, dactyl short and sharp.

Epimeron III posterodistal angle broadly rounded.

Uropod II peduncle subequal to outer ramus, inner ramus slightly shorter than outer, peduncle medial margin and inner ramus with short marginal spines, outer ramus lateral margin with one strong lateral spine in distal half. Uropod III rami subequal, longer than peduncle, outer ramus article 2 very small, inner ramus medial margin with row of long pinnate setae.

Telson ovoid, cleft beyond middle, each lobe with setule notch, lateral margin armed dorsally with row of three short spines.

Remarks

The main distinctive features of the new species (cf. *Scopelocheiropsis abyssalis*, the only other species of the genus) are the following: mandible with cutting edge well developed; coxa I considerably widened distally; pereopods I and II subequal in length, their 6th articles half as long again as the 5th; pereopod II 6th article slightly longer than wide; pereopods III and IV 5th articles relatively long, with triangular anterodistal lobes; pereopods V–VII 2nd articles of different shape, dactyls shorter.

Eurythenes Smith in Scudder, 1882

Eurythenes gryllus (Lichtenstein in Mandt, 1822)

Fig. 4.

Gammarus gryllus Lichtenstein in Mandt, 1822: 34.
Lysianassa magellanica Milne Edwards, 1848: 398.
Eurytenes magellanicus Liljeborg, 1865: 11.
Eurythenes gryllus Smith, 1884: 54. Stephensen, 1933: 12 (partim). Gurjanova, 1951: 265. Birstein & Vinogradov, 1955: 25. Barnard, 1961: 35.
Euryporeia gryllus Sars, 1891–1895: 86. Chevreux, 1900: 24.

Material

TUA 'Sound': st. 2703 (W), N, 995–985 m (30 mfb)—1 juv., 11 mm (SAM–A40882).

Distribution

Meso-, bathy- and abyssopelagic, 5 000–6 000 m. Panoceanic, including the Arctic Basin and the Antarctic, inhabiting middle and near-bottom waters, feeding on carcasses

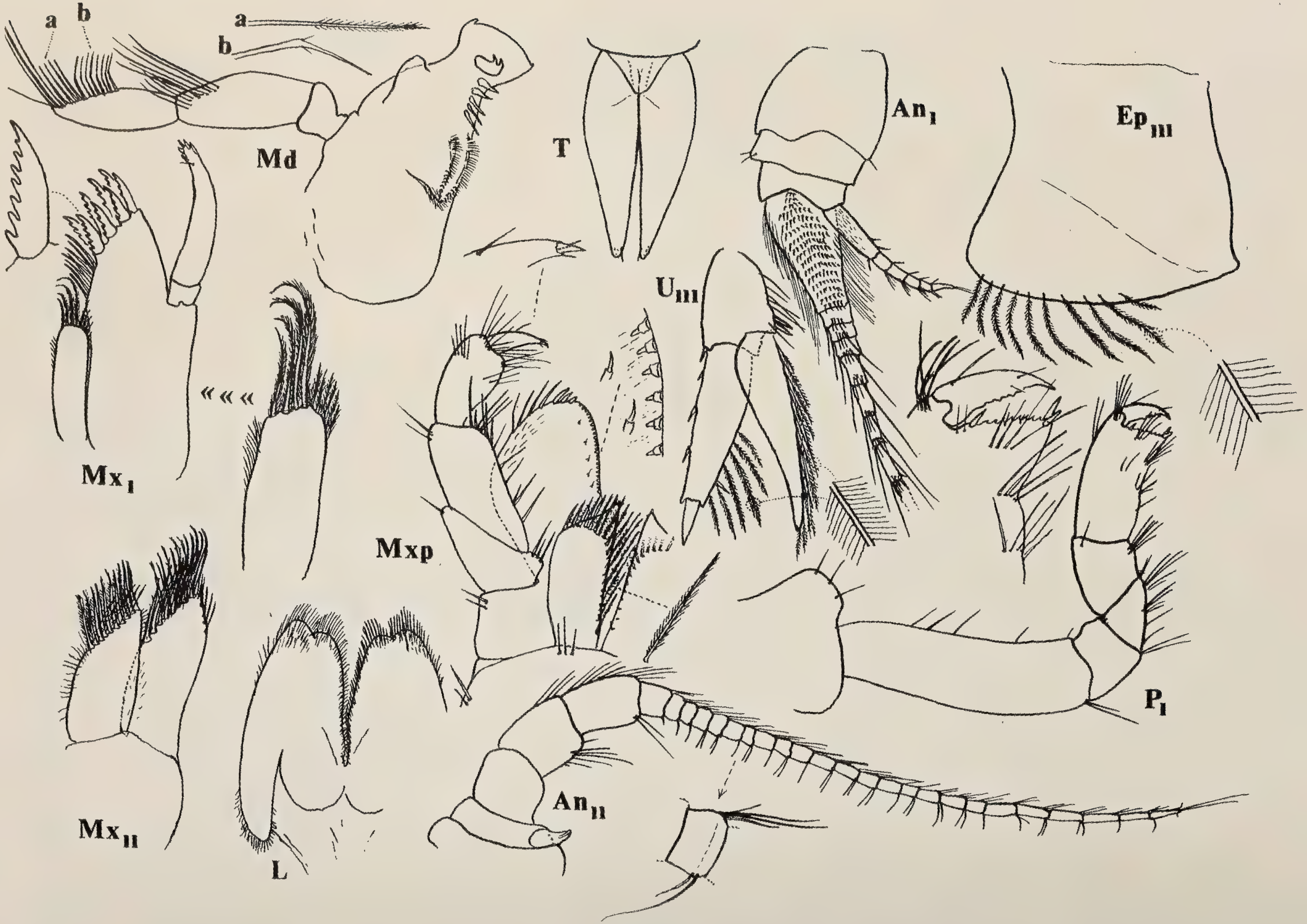

Figure 4
Eurythenes gryllus juv., length 11 mm. St. 2703, TUA 'Sound' (30 mfb).

of fishes and other big animals. It gathers in large numbers on bait. Comparatively large specimens up to 95 mm in length are commonly found in the water column. However, juveniles and very large females (100–120 mm) are recorded only in the near-bottom layers, where they can burrow into the substrate to avoid danger (Birstein and Vinogradov 1958; Baldwin and Smith 1987).

Remarks

Details of morphology of our specimen correspond to existing descriptions and figures of *E. gryllus*, except for two: in contrast to the figure published by Sars (1891–1895) and repeated by Gurjanova (1951), our animal has maxilla II inner and outer plates subequal and maxilliped inner plates with stretched spine-like (not rounded) tops.

Eurythenes obesus (Chevreux, 1905)

Katius obesus Chevreux, 1905*d*: 1. Stephensen, 1933: 12 (partim).

Eurythenes obesus Schellenberg, 1955: 183. Shoemaker, 1956: 177. Birstein & Vinogradov, 1960: 184; 1962: 39; 1964: 163. J. Barnard, 1961: 38.

Material

IKSAMT: st. 2718 (W), N, PT 100 m—1 ♂, 11 mm; st. 2719 (W), N, PT 200 m—1 ♂, 12 mm; st. 2773 (W), N, PT 1 150 m—1 specimen, 11 mm.

Distribution

Cosmopolitan, bathy- and abyssopelagic.

Ichnopus Costa, 1853

Ichnopus pelagicus Schellenberg, 1926

Ichnopus pelagicus Schellenberg, 1926*b*: 218. Birstein & Vinogradov, 1964: 163. Lowry & Stoddart, 1992: 216.

Socarnes longicornis Birstein & Vinogradov, 1960: 185. Gurjanova, 1962: 433.

?*Ichnopus nossibeensis* Ledoyer, 1986: 761.

Material

IKSAMT: st. 2597 (MC), N, NBT 360–550 m—1 ♂, 9.5 mm; st. 2625 (MC), N, NBT 210–220 m—9 specimens, 7–9.5 mm; st. 2799 (SdM), N, NBT 300–200 m—12 specimens, 6–10.5 (♂ reif.) mm; st. 2800 (SdM), N, PT 200 m—1 specimen, 10 mm; st. 2801 (SdM), N, PT 50 m—1 ♂, 8.5 mm.

Distribution

Tropical Pacific and Indian Oceans.

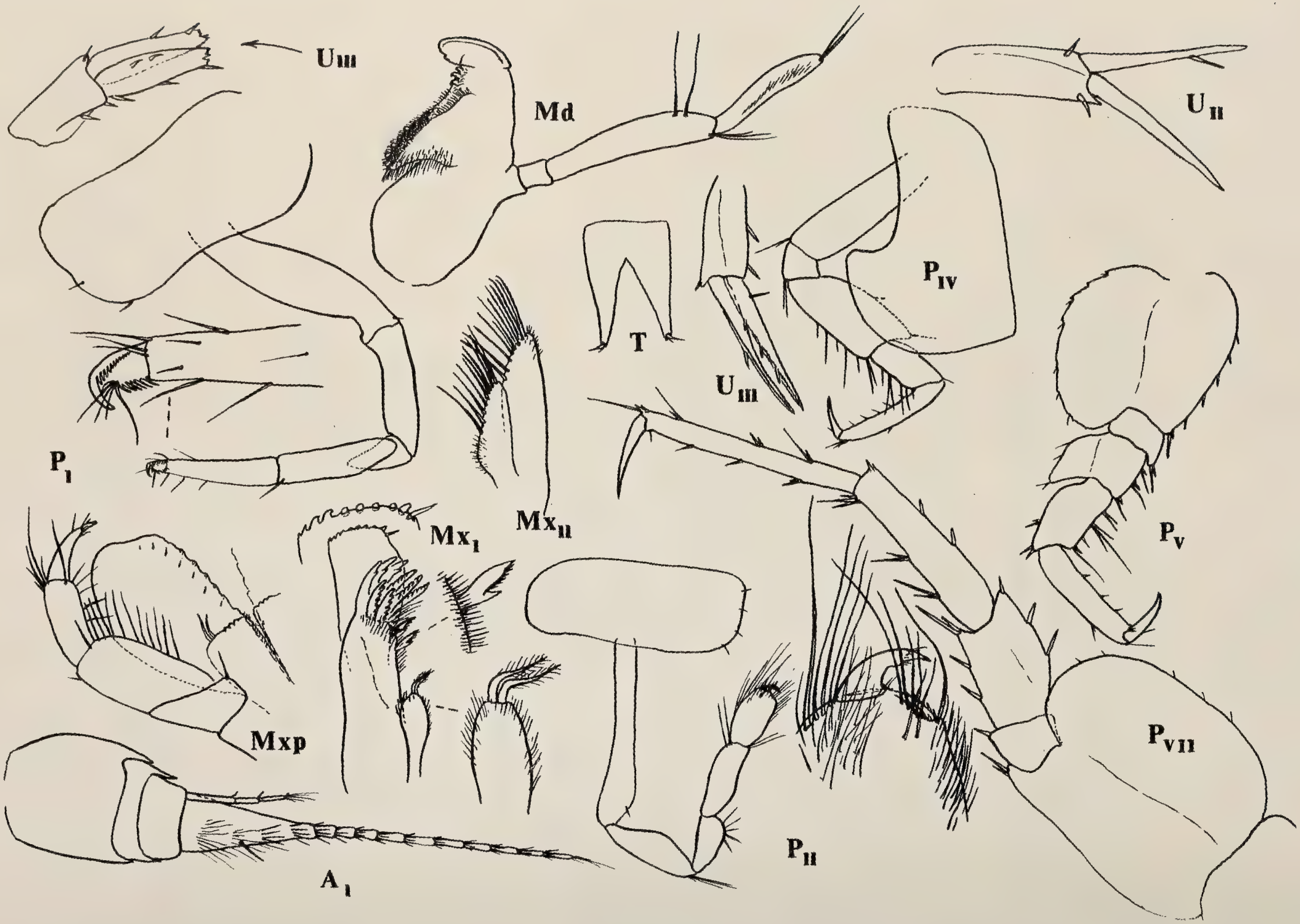

Figure 5
Ichnopus walkeri sp. nov. Holotype.

Ichnopus walkeri sp. nov.

Fig. 5.

Ichnopus taurus Walker, 1904: 238 (*non* Costa, 1853: 72).
Ichnopus sp. Lowry & Stoddart, 1992: 241, fig. 38 (based on Walker's material).

Material

TUA 'Sound': st. 2635 (MC), D, 223 m (2 mfb)—2 juv., 4 mm (holotype, SAM–A40883) and 5 mm (SAM–A40884); st. 2676 (W), D, 1 058–1 068 m (2 mfb)—1 juv., 3.5 mm. One paratype is deposited in the P.P. Shirshov Institute of Oceanology of the Russian Academy of Sciences.

Bottom at st. 2635 and 2676

Muddy.

Etymology

The species was named after Dr A.O. Walker, who first dealt with this animal (see *Remarks*).

Type locality

Mozambique Channel.

Description

Juvenile male 4 mm long. Body smooth, lacking thorns and carina. Eyes large, kidney-shaped, nearly contiguous mid-dorsally. Epistome separated from the upper lip.

Antenna I peduncle barrel-like, 1st article twice as long as 2nd and 3rd taken together, 1st article breadth equal to length; 2nd article shortest. Flagellum proximal articles fused into cone shape, callynophorate, distal part 10-articulate. Accessory flagellum well developed, 3-articulate, 1st article longest. Antenna II slightly longer than antenna I, flagellum 15-articulate, proximal articles with calceoli.

Mandible, incisor, smooth convex, spine row short, molar strong, conical, covered by numerous setae and marginal spines. Palp narrow, weakly armed, slightly longer than mandible itself, attached at level of molar, 3rd article weakly curved, shorter and narrower than linear 2nd article.

Maxilla I inner plate oval with 2 pinnate setae apically, outer plate linear, longer than inner plate; palp 2nd article truncate, apex armed with teeth, 5 small blunt spines and one thick short seta.

Maxilla II inner plate shorter and slightly narrower than outer. Both plates armed by long strong spine-setae.

Maxilliped weakly armed, inner plate reaching apex of palp 1st article, with straight cutting edge distally, bearing small teeth and 2 setae; outer plate petal-like, broadly oval, thin, reaching apex of palp 3rd article, medial margin with submarginal row of short spines; palp greatly exceeding outer plate; dactyl elongate, unguiform, with short nail and accessory setules.

Coxa I deep, with somewhat concave anterior and posterior margins, anterodistal angle rounded. Pereopod I 2nd article about 0.9 times as long as coxa I and subequal to the 5th and 6th articles taken together; 3rd, 5th and 6th articles subequal, 5th article linear, 6th narrow-conical. Dactyl curved, spoon-like, with band of strong setae distally, deeply serrated on both margins with curved hook-like apex. Pereopod II longer than pereopod I, 2nd article slender, subequal to 4th, 5th and 6th articles taken together; 6th article slightly shorter than 5th, oval with short palm.

Pereopods III–IV strong, 4th article 1.6 times as long and 1.8 times as broad as 5th article, slender 6th article subequal to 4th. Coxa IV deep with dorsally subsharp posteroventral lobe.

Pereopod VI longer than V, VII longer than VI, each 2nd article with posteroventral lobe well developed, rounded. Pereopod V has this lobe rounded with very weak sloping teeth. Pereopod V 5th article also with weak posteroventral lobe; 6th article longer than 5th. Pereopods VI and VII 2nd article lobes with straight, smooth posterior margin; 6th article longer than 5th (but not so strong as in pereopod V). 4th articles of pereopods V–VII with parallelogrammiform posteroventral lobes most developed on pereopod V which is 1.7 times broader than long.

Uropod I peduncle larger than rami. Uropod II peduncle and rami subequal. Uropod III peduncle shorter than rami.

Telson lobes triangular, 1.3 times as long as broad basally, cleft per cent of length, each apex with spine and small setule.

Distribution

Also found near Sri Lanka at a depth of about 200 m (Walker 1904; Lowry & Stoddart 1992).

Remarks

Ichnopus walkeri sp. nov. is similar to the group of species which formerly were attributed to the genus *Glycerina* Haswell, 1882. This genus was included into *Ichnopus* in the latest revision (Lowry & Stoddart, 1992). However, all other known species of this group—*I. tenuicornis* (Haswell, 1879), *I. woodmasoni* (Giles, 1890) and *I. teretis* (Andres, 1981)—have deeply indentured article 2 of pereopod V.

The new species is also similar to *I. comorensis* Lowry & Stoddart, 1992, *I. spinicornis* Boeck, 1861 and *I. taurus* Costa, 1853. *Ichnopus comorensis* and *I. spinicornis* differ from *I. walkeri* in having a shorter and distally broadened coxal plate I, short 3rd article of pereopod I and more or less broadly rounded tops of telson's lobes. Also, in *I. spinicornis* 2nd article of pereopod I is broader than in the new species. *Ichnopus taurus* differs from *I. walkeri* in having arming of maxilla I palp (8 separate distal denticles instead of 5 in *I. walkeri* and another indentation of outer distal corner), numerous marginal setae on mandibular palp 3rd article and smaller spines on the mandibular molar.

However, I have no doubt that our specimen belongs to the same species as the animal which was caught near Sri Lanka in 1902 during a cruise of S/S *Lady Havelock,* and was identified by Dr A.O. Walker as *I. taurus* (Walker 1904). Later, Lowry & Stoddart re-examined this specimen and showed that it is not *I. taurus,* and marked it as

Ichnopus sp. (Lowry & Stoddart 1992). Unfortunately, I have not had the opportunity to examine Walker's specimen (Natural History Museum, London; catalogue numbers 1905.2.18:9 and 1905.2.18:304) but fig. 38 and the description in Lowry and Stoddart (1992) helped to resolve this issue.

Thoriella Stephensen, 1915

Thoriella islandica Stephensen, 1915

Thoriella islandica Stephensen, 1915: 39. Shoemaker, 1945: 201. G. Vinogradov, 1990*b*: 41.

Material

IKSAMT: st. 2575 (EM), D, NBT 380–400 m—1♂, 11 mm (SAM–A40885).

Distribution

Cosmopolitan.

Orchomenella Sars, 1895

A few similar genera of lysianassoids (*Orchomene*, *Orchomenella*, *Orchomenopsis*, *Allogaussia*, *Tryphosa*) had been described previously but later, many species with an intergradation of characters were described and Barnard (1964*a*, 1969) declared that all these genera were synonyms of the genus *Orchomene*. Following this, additional revisions were made and the status of some 'old' orchomenoid groups of species changed to subgeneric or generic levels. Now *Orchomenella* is again considered to be a valid genus (Barnard & Karaman 1991; Lowry & Stoddart 1994).

Orchomenella pelagica Birstein & M. Vinogradov, 1960

Orchomenella pelagica Birstein & Vinogradov, 1960: 189.

Material

TUA 'Sound': st. 2676 (W), D, 1 058–1 068 m (2 mfb)—1 specimen, 6 mm.

Bottom at st. 2676

Muddy.

Distribution

Tropical Pacific and Indian Oceans.

Family **Hyperiopsidae**

Parargissa Chevreux, 1908

Parargissa curticornis Birstein & M. Vinogradov, 1960

Parargissa curticornis Birstein & Vinogradov, 1960: 199.

Material

TUA 'Sound': st. 2655 (MC), N, 1 990–1 210 m (30 mfb)–1 ♂ reif., 25 mm (SAM–A40886).

Distribution

Equatorial regions of the West Pacific and Indian Oceans, meso- and bathypelagic.

Family **Stegocephalidae**

Parandania Stebbing, 1906

Parandania boecki (Stebbing, 1888)

Andania boecki Stebbing, 1888: 735.

Parandania boecki Stebbing, 1906: 95. Schellenberg, 1926*a*: 223. K. Barnard, 1932: 77.

Material

IKSAMT: st. 2717 (W), N, PT 1 000 m—1 specimen, 10 mm; st. 2773 (W), N, PT 1150 m—1 specimen, 9 mm; st. 2789 (SdM), N, PT 1 000 m—1 specimen, 13.5 mm. **TUA 'Sound'**: st. 2649 (MC), N, 958–968 m (2 mfb)—1 juv., 2 mm. **BDN 37/50**: st. 2740 (W), N, 250–100 m—1 specimen, 9 mm.

Bottom at st. 2649

Muddy with holes, covered by numerous Hyalospongia (observed on TV monitor of TUA 'Sound').

Distribution

Cosmopolitan, bathypelagic.

Remarks

There are observations showing that *P. boecki* feeds upon Cnidaria, in particular, on the medusae of the genus *Atolla* (Moore & Rainbow 1989; Coleman 1990).

Bathystegocephalus Schellenberg, 1926

Bathystegocephalus globosus (Walker, 1909)

Stegocephalus globosus Walker, 1909: 329.
Stegocephalus valdiviae Strauss, 1909: 72.
Bathystegocephalus globosus Schellenberg, 1926*b*: 221. Birstein & Vinogradov, 1960: 205.

Material

IKSAMT: st. 2675 (W), N, PT 1 000 m—1 specimen, 6 mm; st. 2713 (W), N, PT 200 m—2 specimens, 5 mm each; st. 2714 (W), D, NBT 850–650 m—242 specimens, 4.5–12 mm; st. 2718 (W), N, PT 100 m—5 specimens, 4.5 mm each; st. 2719 (W), N, PT 200 m—32 specimens, 4.5–12.5 mm; st. 2720 (W), D, PT 850–730 m—2 specimens, 7 and 9 mm; st. 2726 (W), N, PT 100 m—5 specimens, 3–7 mm; st. 2727 (W), N, PT 150 m—51 specimens, 4–11 mm; st. 2729 (W), D, PT 620–600 m—2 specimens, 4 mm each; st. 2773 (W), N, PT 1 150 m—7 specimens, up to 13 mm; st. 2775 (W), N, PT 100 m—7 specimens, up to 7 mm; st. 2776 (W), N, PT 200 m—57 specimens, 5–9 mm; st. 2777 (W), N, PT 550 m—9 specimens, up to 9 mm; st. 2785 (SdM), N, PT 600 m—2 specimens, 4 and 11 mm; st. 2787 (SdM), N, PT 100 m—3 specimens, 10 mm each; st. 2788 (SdM), N, PT 400 m—2 specimens, 3 and 7 mm; st. 2805 (SdM), D, NBT 200 m—1 368 specimens, 3–12 mm; st. 2807 (SdM), N, NBT 200 m—18 specimens, 4–8 mm. **TUA 'Sound'**: st. 2757 (W), D, 430–450 m (30 mfb)—1 specimen, 3 mm. **BDN 37/50**: st. 2744 (W), N, 920–500 m—1 specimen, 9 mm.

Distribution

Tropical and subtropical regions in all oceans in the southern hemisphere.

Stegocephaloides Sars, 1895

Stegocephaloides attingens K. Barnard, 1916

Stegocephaloides attingens K. Barnard, 1916: 131.

Material

TUA 'Sound': st. 2647 (MC), N, 402–428 m (2 mfb)—1 juv., 3 mm; st. 2661 (MC), D, 300–258 m (2 mfb)—4 specimens, up to 6 mm. **ODN 80/113**: st. 2648 (MC), N, 450–250 m —1 juv., 2 mm. **BDN 37/50**: st. 2710 (W), N, 450–240 m—1 specimen, 3 mm.

Bottom at st. 2647 and 2661

Muddy, at st. 2647 with numerous holes (observed on TV monitor of TUA 'Sound').

Distribution

South Africa, 250–1 000 m.

Family **Pardaliscidae**

Halice Boeck, 1871

Halice tenella Birstein & M. Vinogradov, 1962

Halice tenella Birstein & Vinogradov, 1962: 49; 1964: 168.

Material

IKSAMT: st. 2799 (SdM), N, NBT 300–200 m (trawl touched the bottom)—1 specimen, 5.5 mm.

Distribution

Indian Ocean in the Southern Hemisphere.

Remarks

Capture of this typically pelagic animal cannot be connected with the trawl touching the bottom.

Halice macronyx (Stebbing, 1888)

Synopioides macronyx Stebbing, 1888: 1000; 1906: 227. Schellenberg, 1926*b*: 225. *Non* K. Barnard, 1930: 363

Halice macronyx Birstein & Vinogradov, 1962: 48.

Material

TUA 'Sound': st. 2637 (MC), N, 930–(0) m (the locking mechanism was out of order)—1 specimen, 7 mm; st. 2746 (W), D, 950 m (30 mfb)—1 specimen, 8 mm.

Distribution

Circumoceanic in the Southern Hemisphere.

Halicoides Walker, 1896

Halicoides discoveryi Thurston, 1976

Halicoides discoveryi Thurston, 1976: 149.

Material

TUA 'Sound': st. 2798 (SdM), N, 230–250 m (30 mfb)—1 ♂, 4 mm (SAM–A40887). **BDN 37/50**: st. 2758 (W), D, 500–250 m—1 specimen, 3 mm.

Distribution

Formerly recorded only in the Atlantic Ocean near the Canary Islands, in the few pelagic hauls from 2 300 to 500 m.

Halicoides tambiella (J. Barnard, 1961)

Pardisynopia tambiella J. Barnard, 1961: 79. G. Vinogradov, 1990*b*: 44.
Halice tambiella Karaman, 1974: 10.
Halicoides tambiella Thurston, 1976: 149.

Material

IKSAMT: st. 2689 (W), D, NBT 500 m (trawl touched the ground)—3 ♂, 5 mm each. **TUA 'Sound'**: st. 2709 (W), N, 530–490 m (30 mfb)—1 specimen, 6 mm; st. 2757 (W), D, 430–530 m (30 mfb)—1 specimen, 5 mm; st. 2797 (SdM), N, 248–258 m (2 mfb)—2 specimens, 4 mm each.

Bottom at st. 2797

Sandy with ripples. One patch of starfishes was observed on TV monitor of TUA 'Sound'.

Distribution

Indo-Pacific.

Remarks

The species was frequently found in benthopelagic trawlings on the Pacific submerged ridges Nazka and Sala-y-Gomez (Vinogradov 1990*b*). However, the type specimen was taken by the grab in the Tasman Sea (Barnard 1961), so this is a true benthopelagic species. The morphology of the present material is comparable with that from the Pacific.

Family **Ampeliscidae**

Ampelisca Kröyer, 1842

The genus includes more than 100 species. The majority are littoral, but 20 species are bathyal and one is abyssal. Commonly ampeliscids live on soft grounds in muddy tubes, often forming dense populations. Observations on *Ampelisca typica*, and a few other species have, however, shown that in the second half of the night ampeliscids vacate their tubes and swim in the plankton, although they do not come near to the sea surface (Mills 1967; Macquart-Moulin 1968; Kaim-Malka 1969; Macquart-Moulin *et al.* 1987).

Ampelisca brevicornis (Costa, 1853)

Araneops brevicornis Costa, 1853: 171.
Ampelisca laevigata Liljeborg, 1855: 123. Sars, 1891–1895: 169.

Tetromatus bellianus Bate, 1856: 58; 1857: 139.
Ampelisca brevicornis Della Valle, 1893: 473 (partim).

Material

TUA 'Sound': st. 2624 (MC), N, 218 m (2 mfb)—1 specimen, 8 mm.

Bottom at st. 2624

Sandy with mud.

Distribution

Cosmopolitan in latitudes below 45°.

Remarks

Very polymorphic species (Schellenberg 1925; Reid 1951).

Family **Synopiidae**

Synopia Dana, 1852

Synopia variabilis Spandl, 1923

Synopia variabilis Spandl, 1923: 18; 1924: 48. J. Barnard, 1965: 494.

Material

Neuston net near underwater lamp at night: st. 2557 (Red Sea, 21°06'N 38°12'E), N, 0–0.5 m—10 specimens, up to 4 mm.

Distribution

Red Sea, Ifaluk and Eniwetok Atolls.

Remarks

Animals reddish in colour, but eggs in marsupiums blue, which is typical of neustonic animals.

Family **Eusiridae**

Eusirus Kröyer, 1845

Eusirus crosnieri Ledoyer, 1978

Eusirus crosnieri Ledoyer, 1978: 369.

Material

IKSAMT: st. 2714 (W), D, NBT 850–650 m (trawl touched the ground)—1 specimen, 7 mm.

Distribution

Mozambique Channel and Madagascar Plateau.

Remarks

See also *Eusirus* sp.

Eusirus sp.

Material

IKSAMT: st. 2823 (EM), D, NBT 390–400 m—1 specimen. **TUA 'Sound'** st. 2655 (MC), N, 1 215–1 220 m (2 mfb)—1 specimen, 5 mm; st. 2660 (MC), D, 133–78 m (2 mfb)—1 exuviae, 17 mm; st. 2709 (W), N, 438–558 m (30 mfb)—1 specimen, 5 mm; st. 2757 (W), D, 490–455 m (2 mfb)—1 specimen, 5 mm.

Bottom

Sandy with mud at st. 2655 and sandy with stones at st. 2757.

Remarks

Specimens damaged, making accurate identification impossible; the species is probably *E. crosnieri*.

Eusiropsis Stebbing, 1899

Eusiropsis riisei Stebbing, 1897

Eusiropsis riisei Stebbing, 1897: 39.

Material

IKSAMT: st. 2576 (EM), D, PT 50–0 m—1 ♂, 8.5 mm; st. 2604 (MC), N, NBT 680 m —1 specimen, 9 mm; st. 2799 (SdM), N, NBT 300–200 m—1 ♀, 8.5 mm and 1 ♂, 9 mm; st. 2805 (SdM), D, NBT 200 m—1 ♂, 11 mm; st. 2827 (EM), N, PT 400 m—2 specimens, 9 and 10 mm.

Distribution

Circumtropical, epipelagic.

Eusirella Chevreux, 1908

Eusirella is a deep-sea genus. As a rule representatives are caught in depths exceeding 800 m (Barnard & Karaman 1991), but in a few cases these amphipods have been reported from subsurface waters, e.g. depths between 200–500 m (Birstein & Vinogradov 1970).

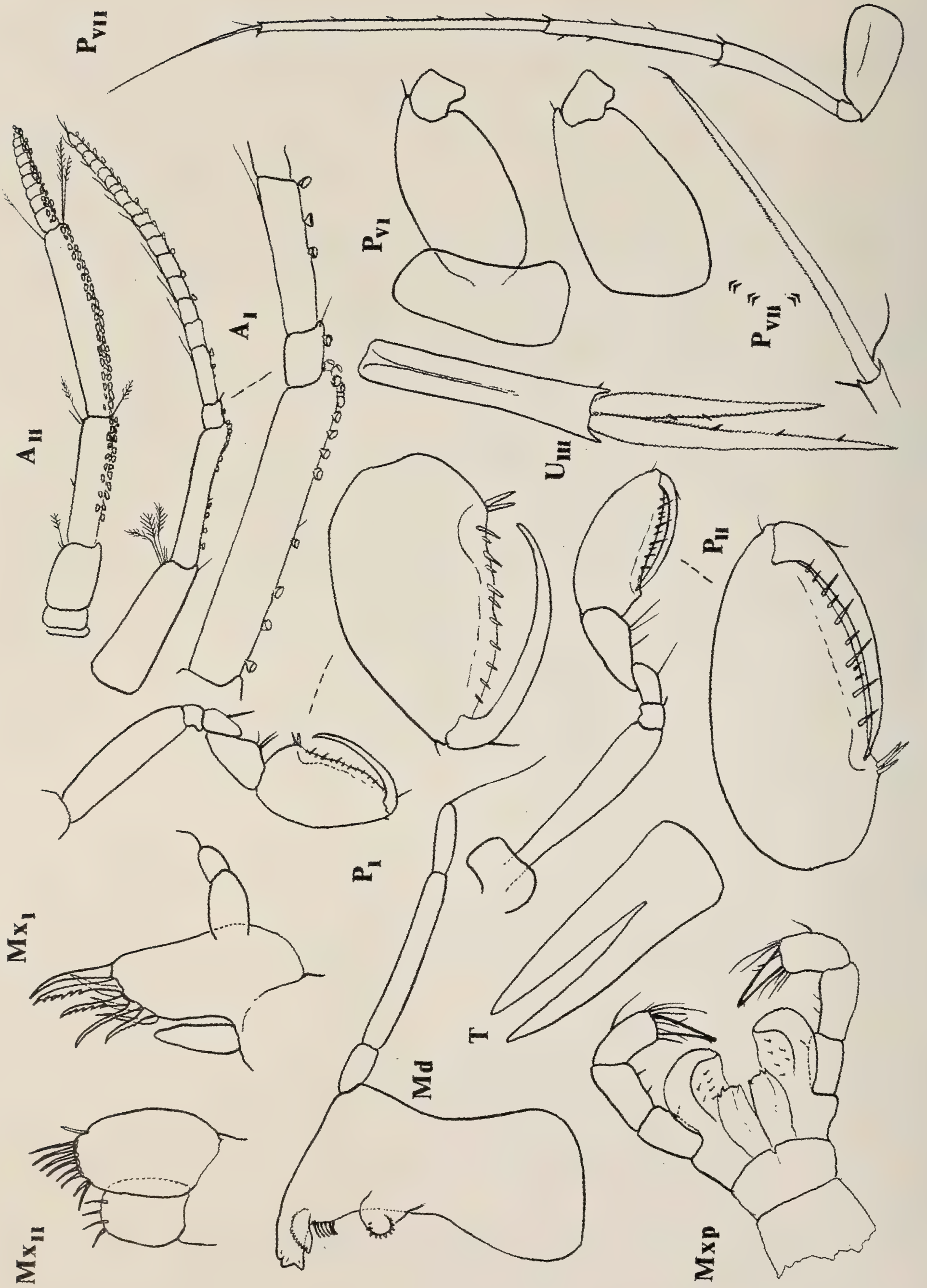

Figure 6
Eusirella ?elegans

Eusirella ?elegans Chevreux, 1908
Fig. 6.

Eusirella elegans Chevreux, 1908: 12; 1935: 103. Shoemaker, 1945: 198 (partim).

Material

TUA 'Sound': st. 2798 (SdM), N, 255–250 m (30 mfb)—2 juv., both 3 mm.

Distribution

North and South Atlantic and western Indian Ocean.

Remarks

The captured amphipods were first juvenile stages. Pereopods I and II had 6th articles particularly short and broad, which is typical of *E. elegans*. They probably belong to this species. However, some differences were also noted: viz. mandibular palp apical article comparatively short and bearing one seta (not two). Maxilliped palp also has noticeably fewer setae than shown by Chevreux's figures. These are interpreted as being merely age-related variability although the possibility that these animals belong to a new species (which is closely related to *E. elegans*) cannot be excluded totally.

Stenopleura Stebbing, 1888

Stenopleura atlantica Stebbing, 1888

Stenopleura atlantica Stebbing, 1888: 950. Stephensen, 1915: 45. Schellenberg, 1926*a*: 353.

Material

IKSAMT: st. 2578 (EM), N, PT 380–400 m—1 specimen, 7 mm; st. 2714 (W), D, NBT 850–650 m—2 specimens, 6 and 6.5 mm. **TUA 'Sound'**: st. 2757 (W), D, 430–530 m (30 mfb)—1 specimen, 5 mm. **BDN 37/50**: st. 2701 (W), D, 750–500 m—1 specimen, 5 mm; ibid., 250–90 m—1 juv., 2 mm; st. 2744 (W), N, 500–250 m—1 ♂, 6.5 mm.

Distribution

Circumtropical.

Remarks

Stenopleura atlantica is normally epipelagic, therefore its capture in closing gear (TUA 'Sound', BDN, but not IKSAMT) at a depth of approximately half a kilometre is worthy of special note.

Stenopleuroides Birstein & M. Vinogradov, 1964

Stenopleuroides macrops Birstein & M. Vinogradov, 1964

Stenopleuroides macrops Birstein & Vinogradov, 1964: 173.

Material

TUA 'Sound': st. 2783 (SdM), D, 262 m (2 mfb)—18 specimens, 2–3 mm; st. 2784 (SdM), D, 263–265 m (30 mfb)—4 specimens, 2–5 mm.

Bottom at st. 2783

Sandy with outcrops of bed rock. Sand with strong ripples; some objects were observed on TV monitor of TUA 'Sound' rolling along the bottom in strong currents.

Distribution

Tropical regions of the Indian Ocean.

Regalia K. Barnard, 1930

Regalia oculata sp. nov.

Figs 7, 8.

Material

IKSAMT: st. 2597 (MC), N, NBT 360–550 m—4 specimens, 7–8.5 (♂) mm (SAM–A40888—SAM–A40891), among them the holotype: ♀ 7 mm (SAM–A40888); st. 2598 (MC), D, PT 400 m—1 juv., 5.5 mm; st. 2799 (SdM), N, NBT 300–220 m—1 ♂, 7 mm (SAM–A40892) and 1 juv., 6 mm. The two last paratypes from stns 2598 and 2799 are stored in the P.P. Shirshov Institute of Oceanology of the Russian Academy of Sciences.

Type locality

Mozambique Channel.

Description

Female 7 mm long. Body with strong cuticle. Pereonite VII, pleonites and urosomite I with big knife-like posteriorly turned dorsal teeth, the biggest one on pleonite II. Pleonites with weak lateral teeth too. Urosomite I with depression. Eyes large, with well marked ommatidia, taking up the major part of the lateral cephalic surface, contiguous dorsally. Rostrum well developed, triangular. Lateral cephalic lobe weak.

Antennae of holotype missing, so this description of the antennae is based on paratype material: specimen SAM–A40889 from st. 2799 (male). Antennae I and II subequal. Antenna I peduncle 1st article massive, rectangular, anterior margin with 8 transverse rows of short setae, 1.5 times longer than wide; 2nd article square, with 5 transverse rows

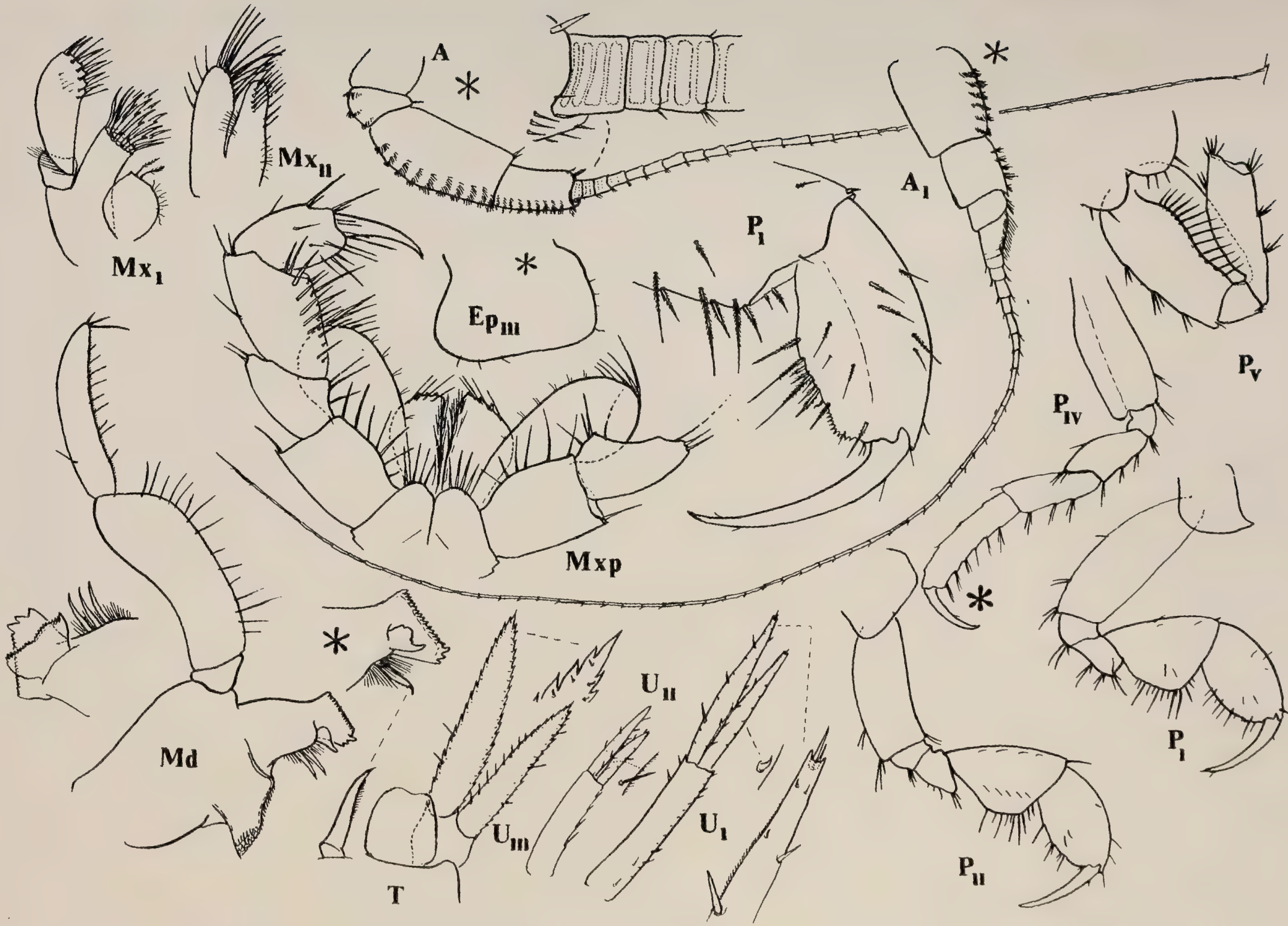

Figure 7
Regalia oculata sp. nov. Holotype and paratype (male, length 7 mm, from st. 2799, marked by *).

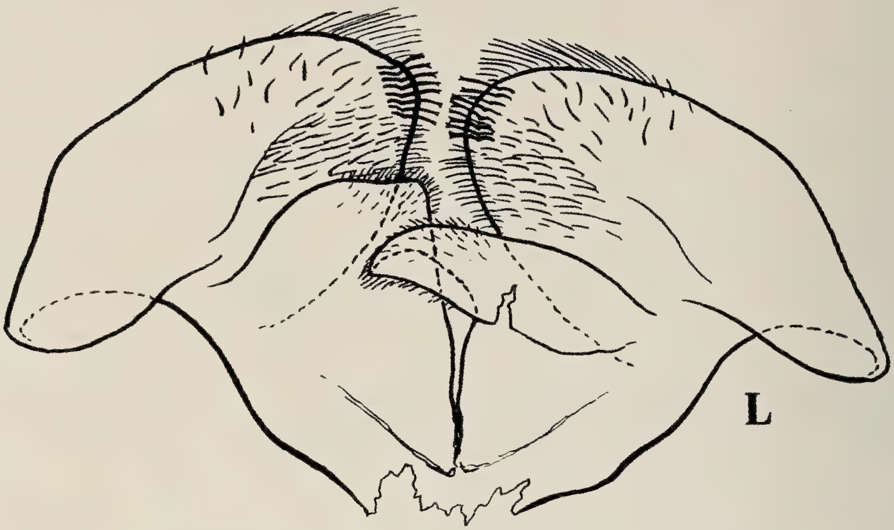

Figure 8
Regalia oculata sp. nov. Paratype (juv., length 5.5 mm, from st. 2598).

of short setae, half as long as 1st; 3rd article short and broad, slightly narrower than 2nd. Flagellum proximal articles merged into a cone, as long as peduncle, covered by weak setae; distal part of flagellum 40-articulate. Accessory flagellum absent. Calceoli absent. Antenna II peduncle articles 1–3 short and broad, 3rd with 4 transverse rows of short setae; 4th article longer than 1–3 combined, rectangular, with 8 transverse rows of short setae; flagellum 40-articulate; calceoli absent.

Lower lip inner lobes well developed, covered by short setules. Outer lobes also covered by short setules, apices have row of strong setae with forked ends. Mandibular processes small, rounded.

Mandible incisor straight, toothed. Right and left laciniae different: right small, with smooth cutting edge and spine-like inner corner; left big, toothed, as broad as incisor, resembling whale’s tail in shape. Spiny row of setae and strong spines (2 and 3 on right and left mandibles of holotype respectively, 1 on some paratype mandibles). Molar conical. Palp strong, longer than the total body of mandible, attached on level with molar, 2nd article slightly longer and twice as broad as 3rd.

Maxilla I palp strong, 2-articulate, with strong setae apically. Inner plate shorter than outer, oval, with sharp apex, resembling a lemon in shape, medial margin armed with two subapical pinnate setae. Maxilla II with inner and outer plates subequal, armed by strong setae.

Maxilliped palp strong, armed with numerous setae, greatly exceeding outer plate, dactyl well developed, ordinary, lacking apical nail. Outer plate oval, reaching to middle of palp 2nd article, apex with 4–5 slender spines, medial margin with row of weak setae. Inner plate reaching apex of palp 1st article, distal margin cutting, armed with 3 short blunt spines and 4 long setae, medial margin with numerous weak setae.

Pereopod I coxa small with acute anterodistal corner, 2nd article slender, a little shorter than 5th and 6th taken together, 5th article trapezoid, extended posteriorly with strong pinnate setae on posterior margin, subequal to 6th. Article 6 oval with long pinnate setae on posterior margin, distal part of palm serrated, dactyl about 90 per cent as long as article 6, overreaching palm. Pereopod II like pereopod I, but coxa without acute anterodistal corner.

Pereopods III–IV slender, article 2 of pereopod III expanded distally with small anterodistal lobe; 4th and 5th articles expanded distally, 6th article slender, about 1.5 times as long as article 5.

Pereopods V–VII 2nd articles broad, with prominent posterolateral lobes. On pereopod V this article has a medial carina bearing a row of long setae, 4th articles rather linear. Unfortunately, pereopods V–VII articles 5–7 were missing in all specimens.

Epimeron III posterodistal angle broadly rounded.

Uropod I peduncle subequal to outer ramus, evenly spinose medially, outer ramus with 3–4 marginal and apical spines, inner ramus shorter than outer ramus. Uropod II peduncle about 1.3 times as long as inner ramus, both rami lanceolate, serrated on both margins. Uropod III peduncle much shorter than rami, rami lanceolate, with serrate margins, inner ramus longer than outer ramus.

Telson subquadrate, entire, somewhat overreaching peduncle of uropod III.

Remarks

The scantily known and poorly defined genus *Regalia* includes two species: *R. fasciculares* Barnard, 1930 described from New Zealand and *R. gracilimana* Pirlot, 1934 from Indonesia. The species considered here does not completely satisfy the generic diagnoses, for specimens possess prominent dorsal teeth on pereonite VII as well as on pleon segments. This feature would put it close to *Halirages* if it were not for the absence of calceoli on the antennae. It differs from *Apherusa* by epimeron III posterior margin smooth. An important distinguishing feature of both these genera is the well developed inner lobe of the lower lip. This and many other features testify to this species being a *Regalia*. The only alternative would be to give it the status of a separate genus, but there is little strength in such an argument.

Regalia oculata may be differentiated from other species in the genus by the above-mentioned teeth on pereonal segment VII and by unusually large eyes. In other respects it is very similar to *R. gracilimana*, especially in the morphology of mouthparts, pereopods III and IV, uropods and telson. However, *R. oculata* possesses epimeron III with posterodistal angle rounded and pereopods I and II with relatively shorter and wider articles 5 and 6.

Paramoera Miers, 1875.

Paramoera austrina (Bate, 1862)
Figs 9, 10.

Atylus austrinus Bate, 1862: 137.
Paramoera australis Miers, 1875: 75. Barnard & Karaman, 1991: 332 (in the list).

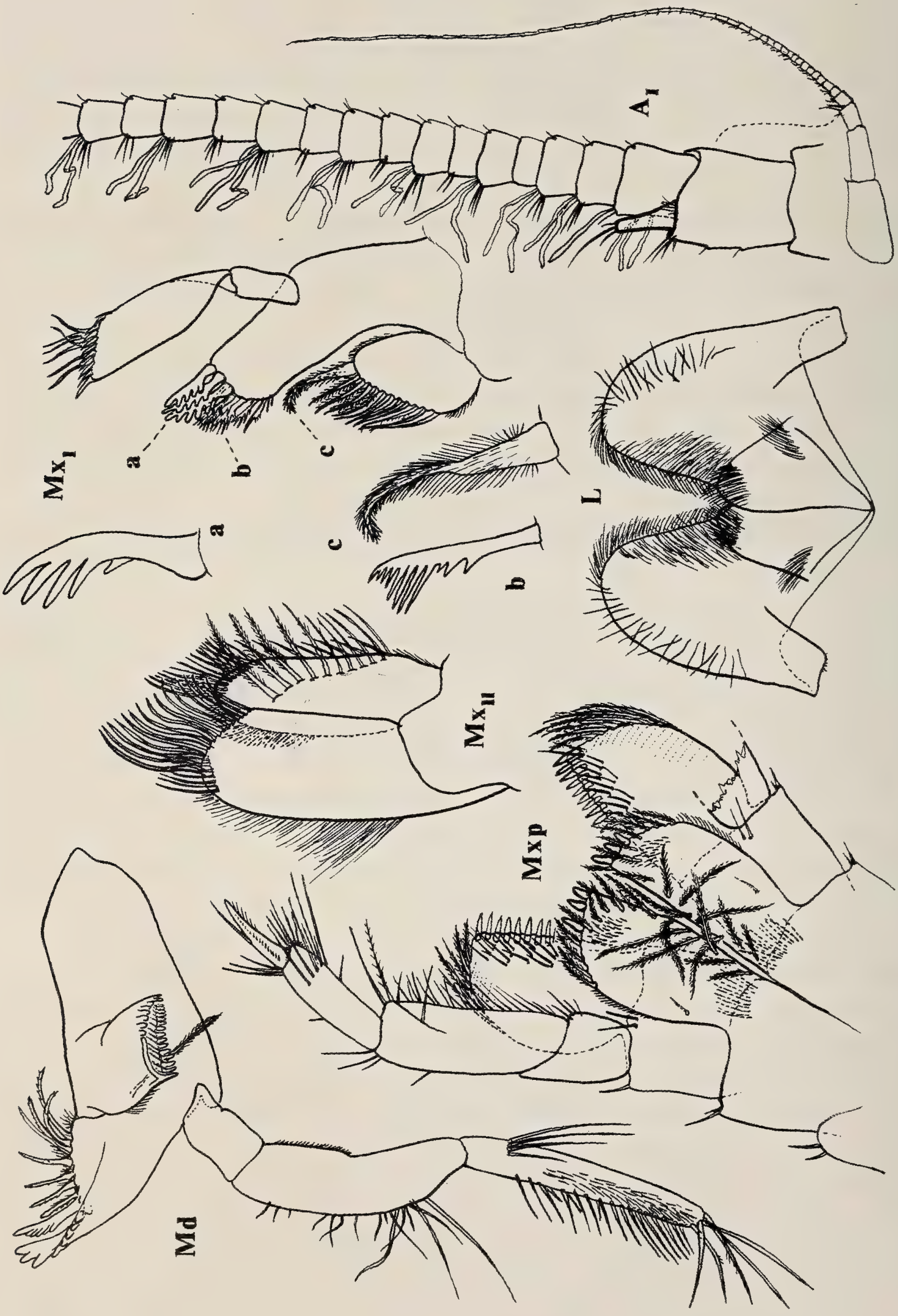

Figure 9
Paramoera austrina, length 6.5 mm. St. 2691, TUA 'Sound' (2 mfb).

Atyloides australis Stebbing, 1888: 914, pts LXXV, LXXVI.
Paramoera austrina Stebbing, 1906: 363. Barnard & Karaman, 1991: 332 (in the list).

Material

TUA 'Sound': st. 2691 (W), N, 28–63 m (2 mfb)—1 specimen, 6.5 mm (SAM–A40893).

Biotope

The bottom was covered with large stones with narrow gaps between them, encrusted by calcareous coralline algae *Mesophyllum syrphetodes* (see also *Biotope* in the description of *Amaryllis maculata* in this article).

Remarks

Our specimen of *P. austrina* conformed to Stebbing's (1888) material, except in a few insignificant details (e.g. pereopods I and II morphology, mandibular palp). However, the drop-like eyes of our specimen are bigger than shown on Stebbing's figures. The eyes take up the majority of the lateral cephalic surface and are nearly contiguous mid-dorsally.

Distribution

South Indian and south Indo-Pacific Oceans.

DISCUSSION

Thirty-four gammaridean species are represented in our material. The overwhelming majority of pelagic gammaridean species are deep-water bathy- and abyssopelagic animals. This explains the paucity of Gammaridea in our epi- and mesopelagic water samples.

Typically epipelagic gammaridean species are few; three of them (*Eusiropsis rissoei*, *Stenopleura atlantica* and *Synopia variabilis*) were found in our material.

The two species of *Trischizostoma*, as has already been pointed out, are ectoparasites of near-bottom sharks which are a consistent element of the fauna of the investigated regions.

Paracyphocaris praedator appears not to be a parasite of sharks, but of large planktonic crustaceans. In addition, *Thoriella islandica* and probably *Parandania boecki,* are parasites/predators of gelatinous zooplankters (Vinogradov 1988; Moore & Rainbow 1989; Coleman 1990).

The remaining 26 species can be categorized into two groups: typical inhabitants of the meso- and bathypelagic zones (it is thought that some of them are able to collect prey from the bottom) and benthic animals only sporadically rising into the pelagial.

Almost all the representatives of the first group are panoceanic species: only *Cyphocaris cornuta* has not been found beyond the waters of the Mozambique Channel. In the IKSAMT samples three species (*Cyphocaris anonyx*, *C. challengeri* and *Bathystegocephalus globosus*) were found in great quantities and amounted to 2.6, 7.5 and

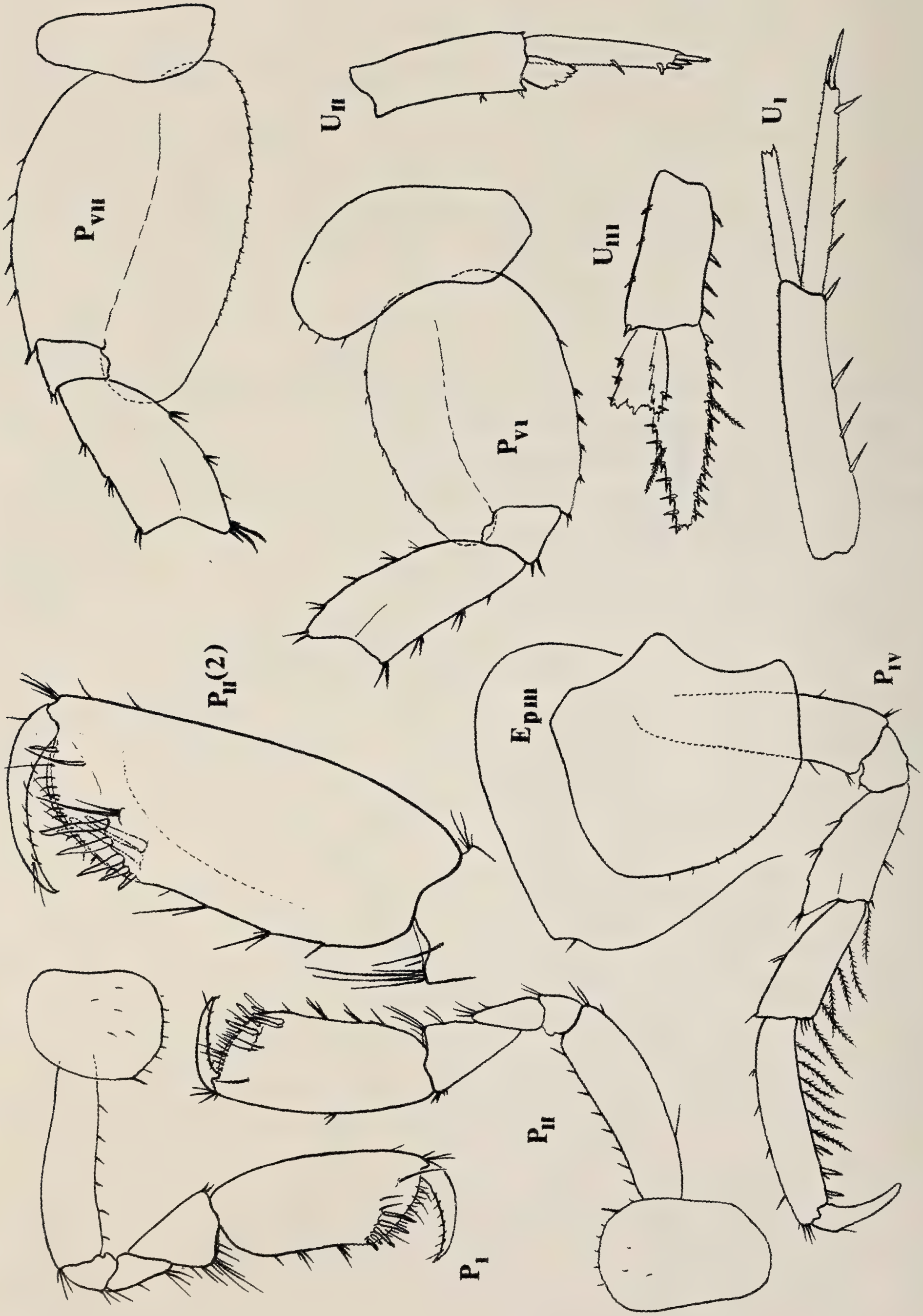

Figure 10
Paramoera austrina, length 6.5 mm. St. 2691, TUA 'Sound' (2 mfb).

79.3 per cent (respectively) of all amphipods so caught. That said, a considerable proportion of *B. globosus* was caught as a result of near-bottom trawling, as will be discussed below.

Comparison of the IKSAMT near-bottom and pelagic samples permits detection of that group of animals which is largely specific to the near-bottom layer of water. Some animals were only recorded (practically) in the near-bottom catches: *Trischizostoma tanjae* (155 out of 156 specimens, recorded in all samples), *Ichnopus pelagicus* (22 out of 24 recorded specimens) and *Regalia oculata* sp. nov. (6 out of 7 recorded specimens). Of these *T. tanjae*, as already indicated, is most likely a parasite of near-bottom sharks, which determines its concentration in this layer. The other two species are free-living animals.

In addition, *Amaryllis maculata* sp. nov., *Erikus dahli*, *Thoriella islandica* and *Halice tenella* were recorded only in the IKŠAMT near-bottom samples. However, these species were represented only by single specimens, which does not permit us to derive any conclusions from these results, especially since all that is known about *T. islandica* and *H. tenella* testifies to the fact that these amphipods were most likely caught during passage of the trawl through the water column.

Bathystegocephalus globosus deserves special mention. This species was regularly (15 times) recorded in the IKSAMT samples; however, its largest numbers were yielded by three near-bottom catches: 242, 1 368 and 18 specimens (out of a total of 1 815 specimens recorded in all catches). Pelagic catches of *B. globosus* were recorded predominantly at night-time (animals were recorded only twice in daytime pelagic samples and in both cases depths exceeding 500 m were being sampled at the time); and most abundant near-bottom trawlings were carried out during the daytime (the richest haul was at a depth of only 200 m). It is possible that *B. globosus* makes active diurnal migrations. At night it may be distributed in the water column and so not abundant in the trawl samples (rarely exceeding 10 specimens per catch). In the daytime the population descends and, if a submerged seamount exceeds this depth, these amphipods accumulate over it. An analogous situation was observed with *Cyphocaris challengeri* over the submerged Nazka and Sala-y-Gomez ridges in the Pacific Ocean (Vinogradov 1990*b*).

Only six gammarideans from five species were found in all the lower (nearest to bottom) plankton net hauls (with lower limit 50 mfb). The TUA 'Sound' catches at 30 mfb yielded 20 gammarideans from 12 species (in 11 from 13 received samples) and 40 gammarideans from 11 species at 2 mfb (in 13 from 35 received samples). Thus, the number of gammarideans increases as one approaches the bottom. The true pelagic amphipods were scare in these samples, the majority were near-bottom and benthopelagic species and benthic migrants. That said, the purely pelagic species were caught in the main at 30 mfb, and benthopelagic and near-bottom gammarideans at 2 mfb (Table 1). *Stenopleuroides macrops* was the only exception to this pattern, 18 out of 22 captured species of this animal were taken at 2 mfb. However, it should be noted that 18 *S. macrops* were caught from one haul (st. 2783, 2 mfb) which may have encompassed a 'swarm'. It is interesting that the opposite pattern, i.e. a sharp decrease in the number of animals on approaching the bottom, appears for the purely pelagic hyperiids and other big planktonic crustaceans on the basis of other results of the same samples (Vinogradov 1990*a*;

Vereshchaka 1990). We observe here one of the specific characteristics of the thin water layer directly overlying the bottom, i.e. a change from the purely pelagic animals to the representatives of the near-bottom plankton.

Comparison of the gammarideans caught by TUA 'Sound' with the other material permits detection of one more group of gammarideans caught only in the near-bottom layer (Table 1, indicated by asterisks). It includes all the benthopelagic and swimming benthic amphipods caught by TUA (except one specimen of *Halicoides discoveryi* and two specimens of *Stegocephaloides attingens* which were also found in the near-bottom catches by the Juday nets covering the 50–250 mfb layer), as well as three species of the typically pelagic amphipods (*Eusirella elegans*, *Stenopleuroides macrops* and *Halice macronyx*). Of the latter, *H. macronyx* and *E. elegans* are rare amphipods represented by one and two specimens (respectively) in the entire sample. Their capture near the bottom is most likely accidental. As for *S. macrops,* it was found in abundance, but only in one place above 300 m depths on the Saya de Malha Bank (12°26–27'S, 61°04'E). Unfortunately pelagic trawling was not carried out at this station, so we have no data on the vertical distribution of this species. Previously, *S. macrops* was recorded in pelagic samples from the upper 300 m layer over depths of 3–4 km (Birstein and Vinogradov 1964).

No significant difference between the number of gammarideans caught during the day or night using TUA 'Sound' has been detected.

TABLE A

IKSAMT station data (stations lacking Gammaridea excluded) 10°25' N

Station No	Date	Local time of trawling	Depth of bottom (m)	Depth of trawling (m)	Location (start point of trawling)	
Error Mountain						
2575	30.X.1988	16.00–17.20	400–1100	380–400	10°18' N	56°06' E
2576	30.X.1988	17.50–18.25	>2000	50–0	10°25' N	56°06' E
2578	31.X.1988	01.45–02.45	1280–1050	380–400	10°18' N	56°17' E
Mozambique Channel						
2597	12.XI.1988	02.35–03.55	390–560	360–550	10°29' S	48°20' E
2598	12.XI.1988	05.15–06.15	560–820	400	12°36' S	48°11' E
2604	13.XI.1988	02.45–03.40	695–690	680	12°31' S	48°09' E
2605	13.XI.1988	11.00–12.30	1100–970	460–700	12°52' S	48°01' E
2616	18.XI.1988	01.45–04.47	3100–3000	1700–1900	15°05' S	42°16' E
2625	22.XI.1988	01.23–02.23	220–230	210–220	24°30' S	35°30' E
2642	28.XI.1988	19.30–21.00	1700–2120	1200	23°21' S	43°23' E
2667	06.XII.1988	17.40–19.00	1900	(100)–200	27°59' S	44°33' E

Station No	Date	Local time of trawling	Depth of bottom (m)	Depth of trawling (m)	Location (start point of trawling)	
Walters Shoal						
2675	10.XII.1988	03.21–04.21	1600–1320	1000	32°54' S	45°23' E
2689	12.XII.1988	16.45–18.38	250–600	0–500–0	33°16' S	43°50' E
2712	16.XII.1988	00.22–01.22	550–600	100	33°08' S	43°59' E
2713	16.XII.1988	02.10–03.00	650	200	33°12' S	43°59' E
2714	16.XII.1988	05.20–06.35	850–790	850–650	33°22' S	43°51' E
2717	16.XII.1988	22.40–23.30	2400	1000	34°06' S	43°45' E
2718	17.XII.1988	01.10–02.10	2400	100	34°00' S	43°45' E
2719	17.XII.1988	03.10–04.13	2200–1600	200	33°55' S	43°46' E
2720	17.XII.1988	05.30–06.45	1600–2000	850–730	33°50' S	43°47' E
2725	18.XII.1988	00.17–01.17	50–30	20	33°11' S	43°52' E
2726	18.XII.1988	01.51–02.51	220–750	100	33°16' S	43°54' E
2727	18.XII.1988	03.30–04.30	750–920	200–150	33°24' S	43°56' E
2729	18.XII.1988	07.25–08.25	1150–1580	620–660	33°33' S	43°55' E
2773	25.XII.1988	19.21–20.21	2040–2100	1150	31°25' S	45°56' E
2775	25.XII.1988	22.36–23.36	2150–2200	100	31°17' S	46°09' E
2776	26.XII.1988	00.08–01.08	2200	200	31°13' S	46°12' E
2777	26.XII.1988	02.00–03.00	2200	550	31°08' S	46°15' E
Saya de Malha Bank						
2785	05.I.1989	20.20–21.20	1600–1900	600	12°22' S	60°49' E
2787	05–06.I.89	23.17–00.17	1900–2200	100	12°13' S	60°41' E
2788	06.I.1989	01.08–02.08	2200–2000	400	12°09' S	60°40' E
2789	06.I.1989	03.58–04.58	2000–2115	970–1020	12°03' S	60°38' E
2794	06.I.1989	15.00–16.00	303–700	300–330	11°49' S	60°58' E
2799	06–07.I.89	23.50–00.50	310–220	300–220	11°49' S	61°00' E
2800	07.I.1989	01.43–02.43	250	200	11°45' S	61°05' E
2801	07.I.1989	03.12–03.42	250–238	50	11°41' S	61°09' E
2805	07.I.1989	15.57–17.00	240–223	230–200	11°12' S	62°11' E
2807	08.I.1989	02.35–03.35	215–190	210–185	11°08' S	62°12' E
Error Mountain (second visit)						
2823	14.I.1989	15.55–16.55	390–432	380–400	10°19' N	56°06' E
2826	14.I.1989	21.20–22.20	400	390–370	10°18' N	56°04' E
2827	15.I.1989	00.00–01.00	2000	370	10°22' N	56°04' E

TABLE B

TUA ‘Sound’ station data (stations lacking Gammaridea excluded)

Station No	Date	Local time of sampling	Depth of bottom (m)	Location (start point of catching)	
Mozambique Channel					
2624	21–22.XI.1988	23.45–00.15	220–220	24°31' S	35°28' E
2635	25.XI.1988	14.01–14.30	223–223	25°11' S	35°13' E
2637	26.XI.1988	02.13–04.30	975–910	25°18' S	35°24' E
2647	2.XII.1988	19.08–21.08	404–521	22°17' S	43°04' E
2649	3.XII.1988	01.06–03.06	965–950	22°22' S	43°00' E
2655	3.XII.1988	19.17–21.17	1215–1240	22°26' S	42°53' E
2660	4.XII.1988	10.14–10.44	135–80	22°12' S	43°09' E
2661	4.XII.1988	11.30–12.30	312–180	22°13' S	43°07' E
Walters Shoal					
2676	10.XII.1988	09.15–11.15	1060–1070	32°55' S	44°39' E
2678	10.XII.1988	18.23–20.23	850–790	33°03' S	44°12' E
2681	11.XII.1988	01.55–03.55	510–340	33°09' S	43°58' E
2691	12–13.XII.88	23.40–00.40	46–30–76	33°09' S	43°53' E
2709	15.XII.1988	18.08–20.08	455–590	33°09' S	43°58' E
2737	19.XII.1988	14.50–16.50	1100–1113	33°58' S	45°04' E
2746	21.XII.1988	07.20–09.20	980–950	33°47' S	44°35' E
2757	23.XII.1988	05.35–07.35	485–560	33°15' S	43°57' E
Saya de Malha Bank					
2783	5.I.1989	14.54–15.54	265	12°26' S	61°04' E
2784	5.I.1989	16.45–17.15	268–275	12°27' S	61°04' E
2792	6.I.1989	12.10–12.40	296	11°49' S	61°00' E
2797	6.I.1989	20.57–21.27	250–260	11°46' S	60°59' E
2798	6.I.1989	21.43–22.13	260–285	11°47' S	61°00' E

TABLE C

BDN station data (stations lacking Gammaridea excluded)

Station No	Date	Local time of sampling	Haul (m)	Depth of bottom (m)	Location	
2701	14.XII.1988	15.05–15.40	750–500	820	33°03' S	44°05' E
"		16.15–16.22	250–90			
2710	15.XII.1988	21.30–22.10	450–240	500	33°07' S	43°56' E
2740	19.XII.1988	20.30–20.50	250–100	990	33°55' S	44°55' E
2744	21.XII.1988	03.55–04.50	920–500	970	33°47' S	44°35' E
"		04.55–05.25	500–250			
2758	23.XII.1988	08.53–09.20	500–250	550	33°17' S	43°56' E

TABLE D

ODN station data (stations lacking Gammaridea excluded)

Station No	Date	Local time of sampling	Haul (m)	Depth of bottom (m)	Location	
2586	03.XI.1988	03.15–03.45	500–250	750	00°27' N	56°03' E
2648	02.XII.1988	21.45–22.10	450–250	520	22°21' S	43°04' E
2656	03.XII.1988	21.17–22.55	1000–500	1270	22°20' S	42°54' E

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ANNALS OF THE SOUTH AFRICAN MUSEUM

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MYSIDACEA FROM THE COMOROS ARCHIPELAGO WITH DESCRIPTIONS OF TWO NEW SPECIES

by

TRIS WOOLDRIDGE
&
JAN MEES

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MYSIDACEA FROM THE COMOROS ARCHIPELAGO WITH DESCRIPTIONS OF TWO NEW SPECIES

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(With 7 figs & 1 table)

[MS accepted 7 September 2003]

ABSTRACT

Five species of *Anisomysis* were collected from a coral reef flat on Grande Comore, Western Indian Ocean. *Anisomysis hanseni* Nouvel, 1967, *A. marisrubri* Băcescu, 1973*a* and *A. vasseuri* Ledoyer, 1974 represent new distribution records for the three species. Two new species are described. *Anisomysis unispinosa* sp. nov. is distinguished by the presence of a single spine at the distal end of the telsonic lobes of the deeply cleft telson. *Anisomysis comorensis* sp. nov. is distinguished by the truncate distal border of the telson and its armature.

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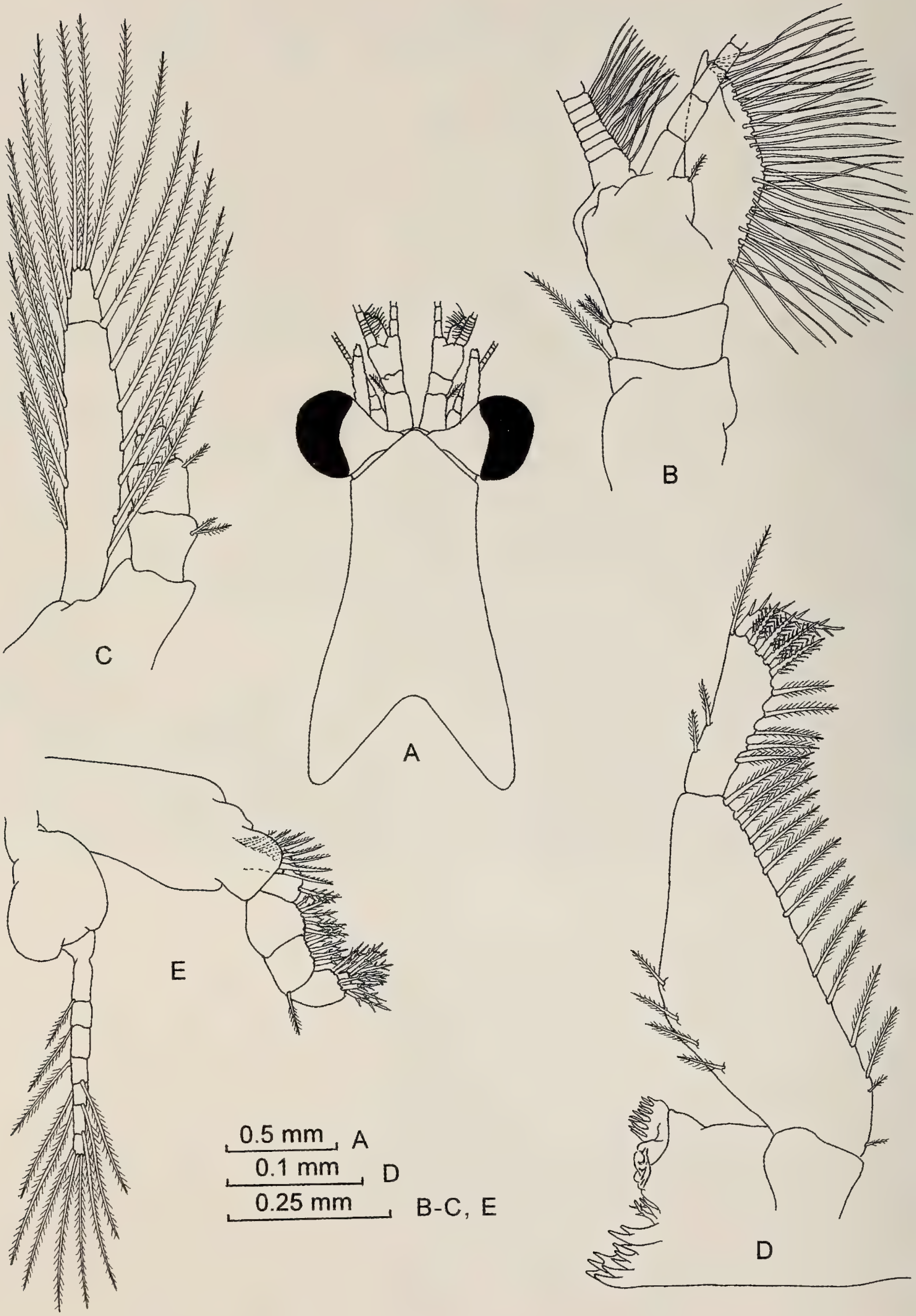

Figure 1
Anisomysis unispinosa sp. nov.
Adult male: (A) anterior part of body and carapace in dorsal view. (B) antennule. (C) antenna. (D) mandible. (E) first thoracic limb.

INTRODUCTION

The Comoros group of four main islands lies approximately equidistant from the African mainland and Madagascar in the northern sector of the Mozambique Channel. Grande Comore is the largest (950 km^2) of these volcanic islands. Although fringing coral reefs line about 60% of the 170 km perimeter of Grande Comore, reefs are small and discontinuous (Quod *et al*. 2000).

No mysids are currently known from this archipelago. The present paper describes two new species of *Anisomysis* from Le Galawa coral reef flat (water depth 4–5 m at high tide) at the northern tip of Grande Comore (Njazidja). *Anisomysis marisrubri* Băcescu, 1973*a*, *A. hanseni* Nouvel, 1967 and *A. vasseuri* Ledoyer, 1974 were also common in samples, extending their previous known ranges (see Table 1, page 101). *Anisomysis marisrubri* was also recently recorded from Mozambique (Wooldridge & Mees 2003), while the second author collected the species in 1994–96 over weed beds at Gazi Bay, providing the first Kenyan record of distribution.

Deprez *et al*. (2001) list 43 species of *Anisomysis*. To this list must be added *A. ijimai* Nakazawa, 1910, *A. mixta australis* Zimmer, 1918, Băcescu, 1973*b*, *A. spatulispina* Murano, 1995*b* and *A. nana* Murano, 1995*b*. A further three species are supplementary: *Anisomysis arabicus* from coastal waters of Oman (Wooldridge & Victor 2004) and the two new species described in this paper. Although members of the genus occur in the warm-water regions of the Indo-West Pacific (Murano 1995*a*), only 15 of the 50 known species occur in the Western Indian Ocean (Table 1).

Samples at Grande Comore were collected at night with a small benthic sled towed over scattered patches of low reef, interspersed with patches of coral sand and weed. Type specimens are lodged in the South African Museum, Iziko Museums of Cape Town.

DESCRIPTION OF MATERIAL

Anisomysis unispinosa sp. nov.
Figs 1–4

Type species

SAM–A45145. Adult male from Le Galawa reef flat on Grande Comore (11°22'07"S, 43°19'13"E). Collected by T. Wooldridge, 28 October 1997.

Paratypes

SAM–A45146. Three adult males and three adult females.

Description

Morphological characteristics described refer to both sexes, unless otherwise stated. Carapace short, posterodorsal margin emarginated and rounded medially (Fig. 1A). Frontal margin produced into short rostrum covering the base of eyestalks; apex narrowly

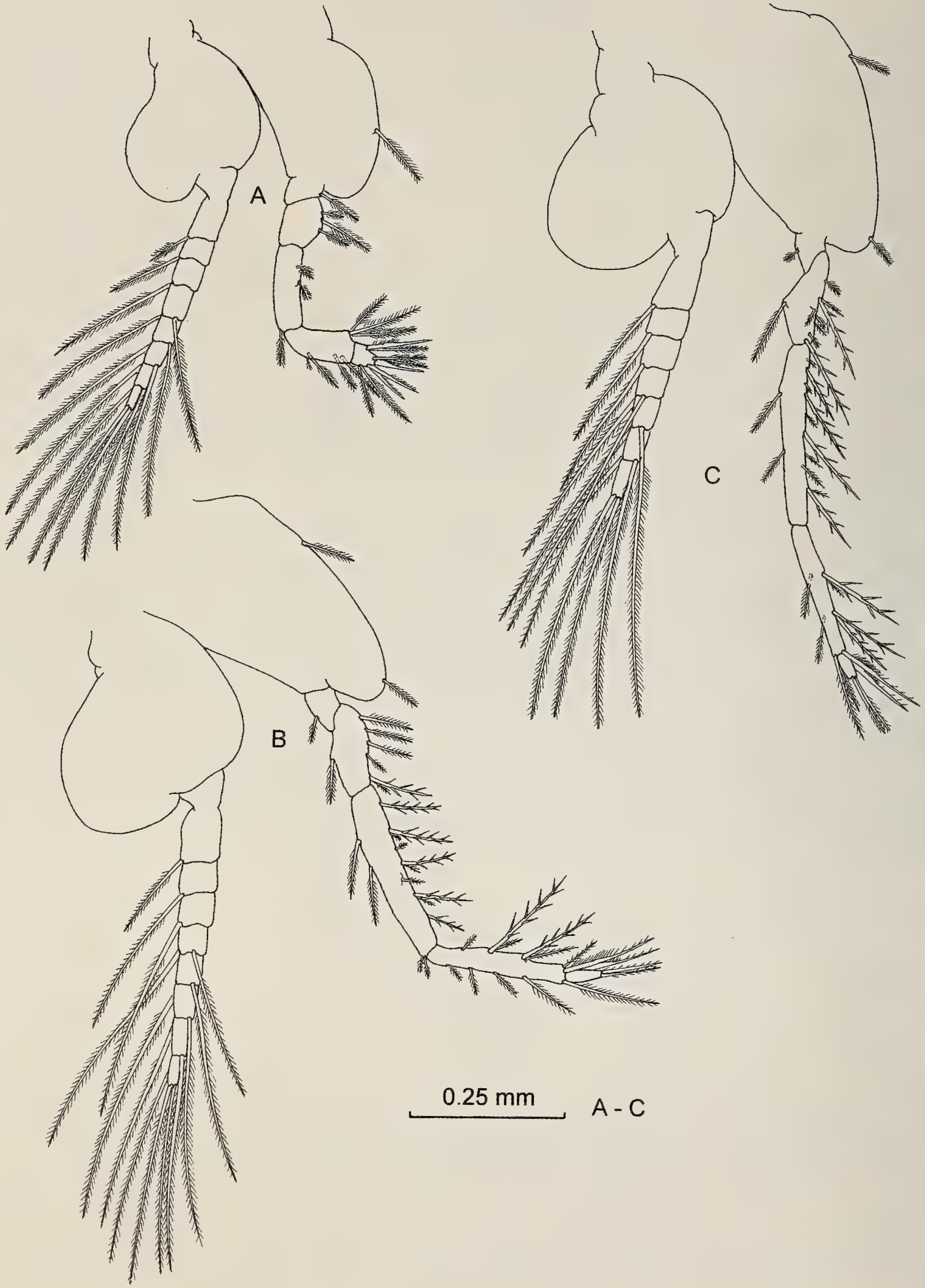

Figure 2
Anisomysis unispinosa sp. nov.
Adult male: (A) second thoracic limb. (B) fourth thoracic limb. (C) fifth thoracic limb.

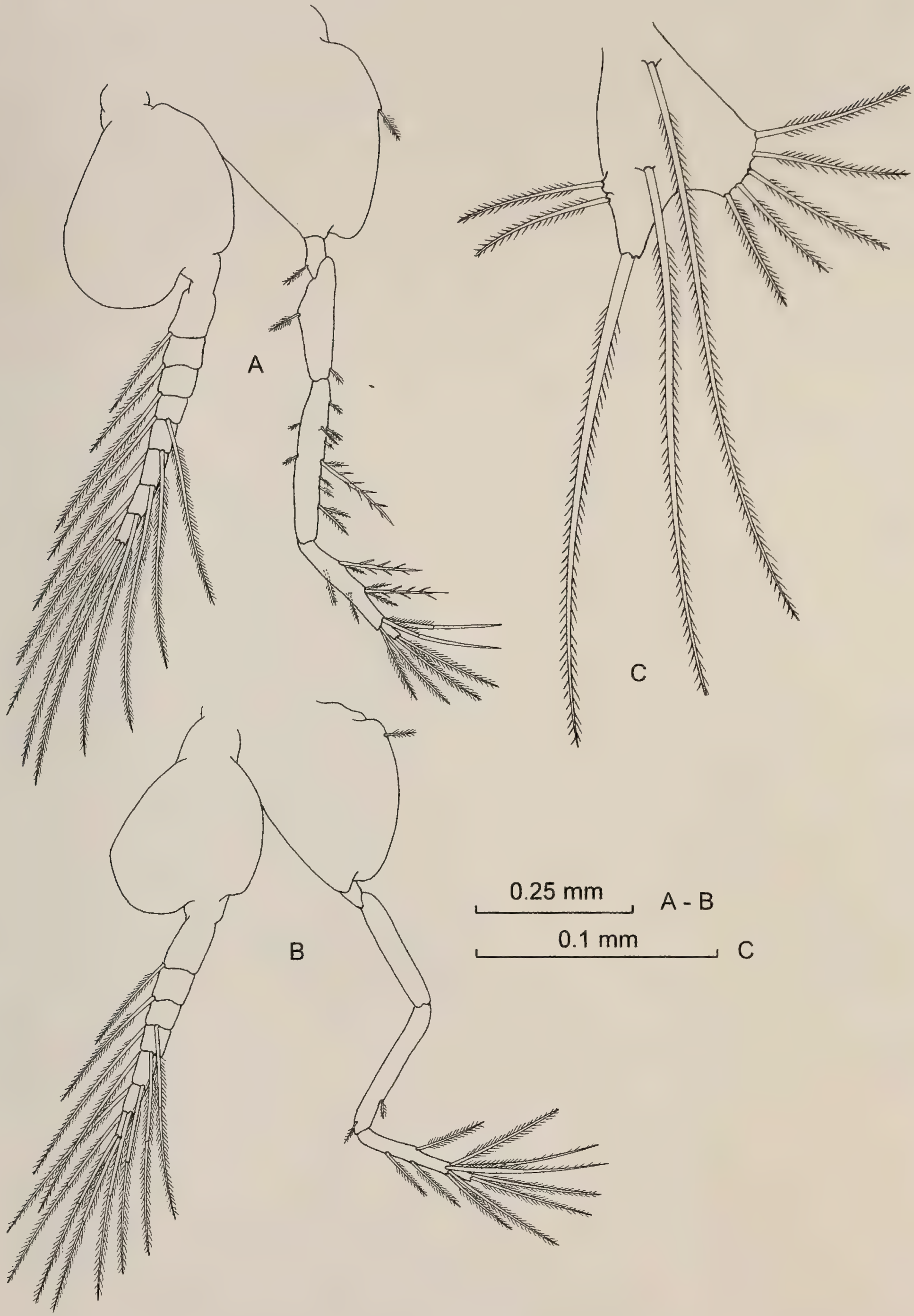

Figure 3
Anisomysis unispinosa sp. nov.
Adult male: (A) seventh thoracic limb. (B) eighth thoracic limb. (C) first pleopod.

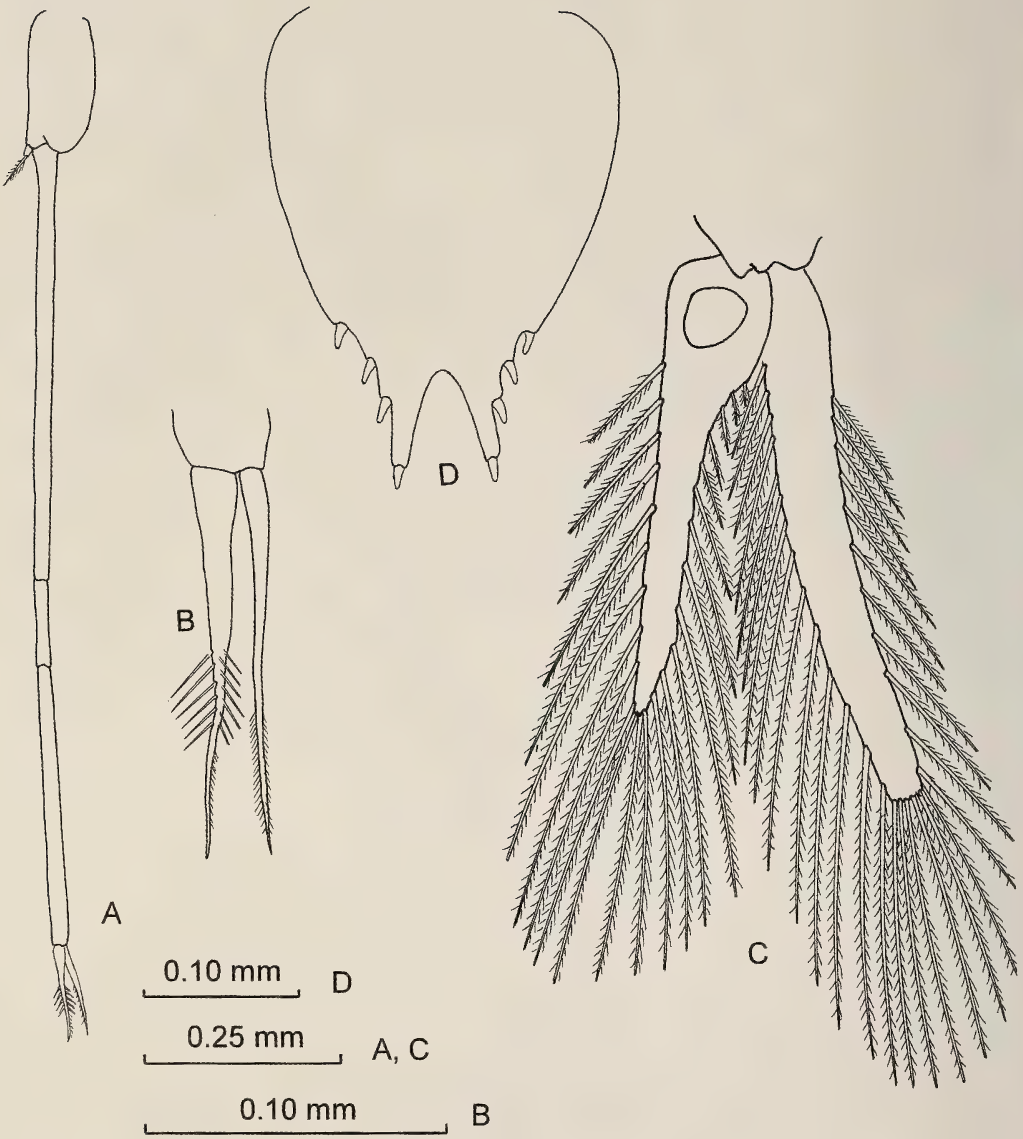

Figure 4
Anisomysis unispinosa sp. nov.
Adult male: (A) fourth pleopod. (B) distal end of exopod of fourth pleopod. (C) uropod. (D) telson.

rounded. Eyes longer than broad, projecting well beyond lateral margin of carapace. Cornea wider than eyestalk.

Antennular peduncle more robust in male than in female; in male first article (Fig.1B) equal in length to third article, armed at outer distal angle with a long seta. Second article twice as broad as long, bearing two short setae on outer distal margin; third segment with well developed hirsute lobe.

Antennal scale (Fig. 1C) extending slightly beyond distal end of antennular peduncle, nearly six times long as broad, setose all round, suture present at distal sixth. Antennal peduncle short, not reaching midlength of scale.

Second article of mandibular palp (Fig. 1D) 2.3 times long as broad and without denticles, inner and outer margin bearing four and 15 setae as illustrated; third segment less than half length of second with comb-like process at distal end.

Endopod of first thoracic limb (Fig.1E) shorter and more robust compared to endopod of second limb (Fig. 2A). Endopod of third limb more slender than that of second limb. Remaining limbs with endopod similar in length (Figs 2B, C, 3A, B), carpopropodus undivided. Ischium shorter than merus on all thoracic endopods, but gradually increasing in relative length posteriorly. Eighth thoracic endopod (Fig. 3B) relatively slender, sparsely setose. Basal segment of exopod expanded (Figs 1E, 2A–C, 3A, B) rounded on outer distal angle. Exopod flagellae 7 or 8 segmented, each segment with one or two plumose setae as illustrated.

First three pairs of pleopods in male similar in form, the first (Fig. 3C) the largest and bearing 3 long setae and two groups of short setae as illustrated. Fourth pair biramous, endopod small (Fig. 4A); exopod three-segmented and reaching beyond base of telson, first segment 5.1 and 1.5 times longer than second and third segments respectively, third segment 3.3 times longer than second, terminating in two stiff setae (Fig. 4B). Female pleopods rudimentary.

Uropods long and narrow, setose all round; exopod longer than endopod and curved slightly outward (Fig. 4C). Exopod of uropod nearly three times length of telson.

Telson 1.25 times as long as basal width (Fig. 4D), bifurcate distally. Cleft one-fifth length of telson, unarmed and rounded at bottom. Lateral margins convex in proximal two-thirds, distal one-third concave, armed with three small spines. Last lateral spine located along margin of lobe of telson, lobes slightly tapering and divergent, each lobe terminating in a single spine.

Length: adult male 3.3–4.1 mm; adult female 3.3–4.2 mm.

Etymology

The specific name refers to the single spine on each lobe of the telson.

Remarks

Anisomysis unispinosa sp. nov. is readily distinguished from allied *Anisomysis* species by the shape and armature of the telson. In *A. unispinosa* sp. nov., the telson is deeply cleft and divergent, without spines around the cleft margin. There are only three pairs of lateral spines located opposite the base of the cleft. All spines on the telson are also of similar length.

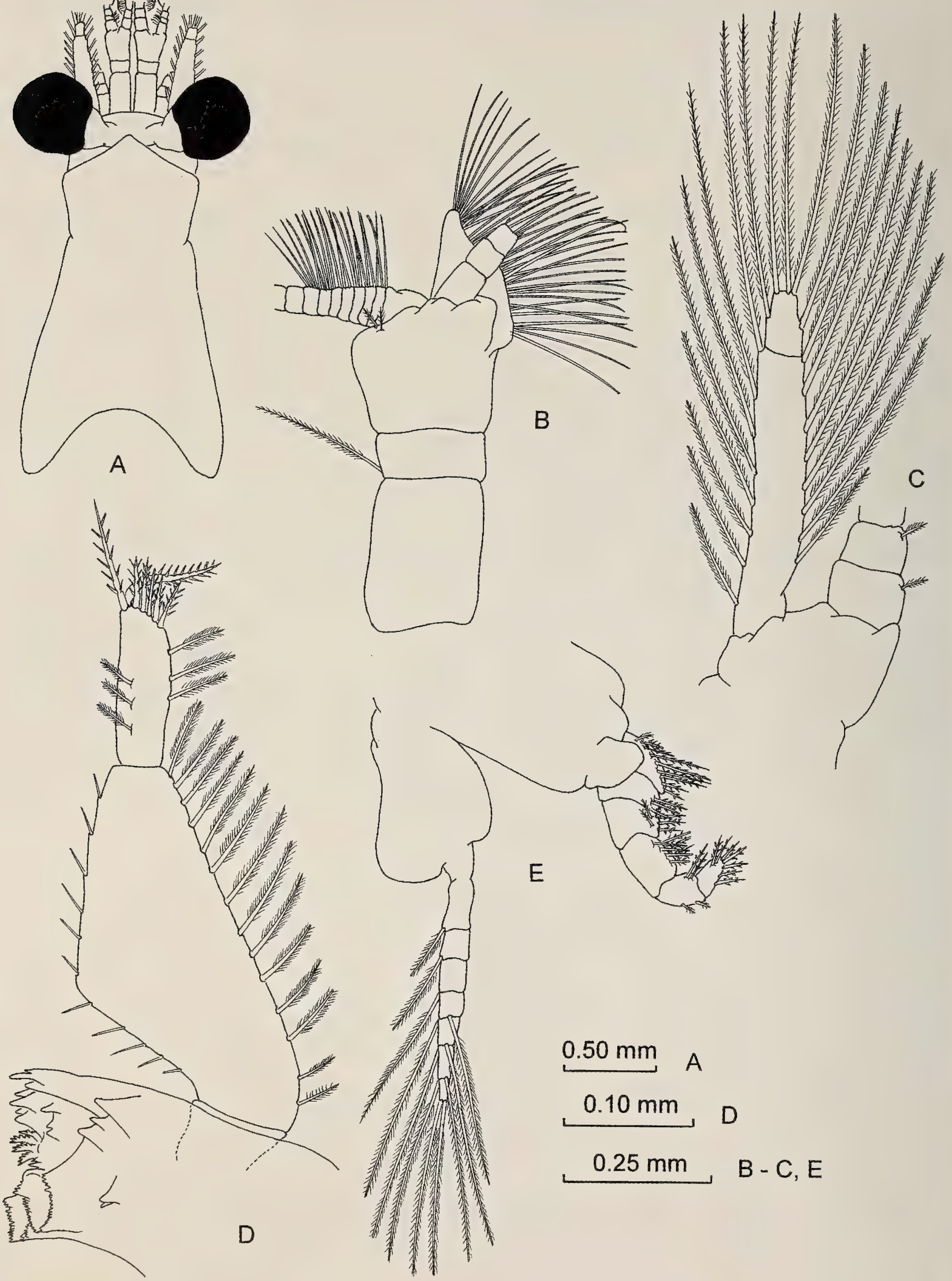

Figure 5
Anisomysis comorensis sp. nov.
Adult male: (A) anterior part of body and carapace in dorsal view. (B) antennule. (C) antenna. (D) mandible. (E) first thoracic limb.

The new species is most similar to *Anisomysis kunduchiana* Băcescu (1975) in the shape and armature of the telson recorded from coastal waters of Tanzania, but the latter differs in having two apical spines on the telsonic lobes. Another clearly distinguishing feature refers to the fourth male pleopod; in *A. unispinosa* sp. nov., the third article of the exopod segment is relatively long when compared to the first segment (> half the length or *c.* 0.67 times by comparison) while in *A. kunduchiana* the third segment is < half the length of the first segment (*c.* 0.48 times length).

Anisomysis comorensis sp. nov.

Figs 5–7

Type species

SAM–A45147. Adult male from Le Galawa reef flat on Grande Comore (11°22'07"S, 43°19'13"E). Collected by T. Wooldridge, 28 October 1997.

Paratypes

SAM–A45148. Three adult males and three adult females from the same locality.

Description

The morphological characteristics described refer to both sexes, unless otherwise stated. Carapace short (Fig. 5A), slightly produced anteriorly into a triangular, obtusely pointed rostrum; extending to base of eyestalks. Posterior border of carapace emarginate and smoothly rounded, exposing last three thoracic somites. Eyes large, projecting well beyond lateral margins of carapace. Cornea wider than eyestalk.

Antennular peduncle more robust in male than in female; in male first article (Fig. 5B) slightly longer than third article, armed at outer distal angle with a long seta. Hirsute lobe well developed, incised on inner margin. Second article twice as wide as long.

Antennal scale (Fig. 5C) in male extending to distal end of antennular peduncle (Fig. 5B), nearly seven times long as maximum width. Lateral margins of scale curved slightly outwards, armed with *c.* 9–10 plumose setae on either side. Distal suture present at distal sixth. Antennal peduncle short, not reaching midlength of scale.

Second article of mandibular palp (Fig. 5D) slightly more than twice as long as broad, inner margin sharply angled, not bearing denticles, with *c.* 11 setae. Outer margin almost straight, bearing *c.* 14 setae along margin. Third article 2.8 times long as broad, with a terminal comb-like process and *c.* six barbed spines. Lateral margins of segment with six setae as illustrated.

Endopod of first thoracic limb (Fig. 5E) short and more robust compared to endopod of second thoracic limb (Fig. 6A). Remaining thoracic limbs similar in form, endopod becoming progressively less setose posteriorly (Fig. 6B, C); carpopropodus undivided. Basal article of exopod expanded, rounded on outer distal angle, flagellate part 7 or 8 segmented.

First three pairs of male pleopods similar in form; first pleopod (Fig. 7A) largest and bearing three long setae and sets of four, one or two shorter setae as illustrated. Fourth

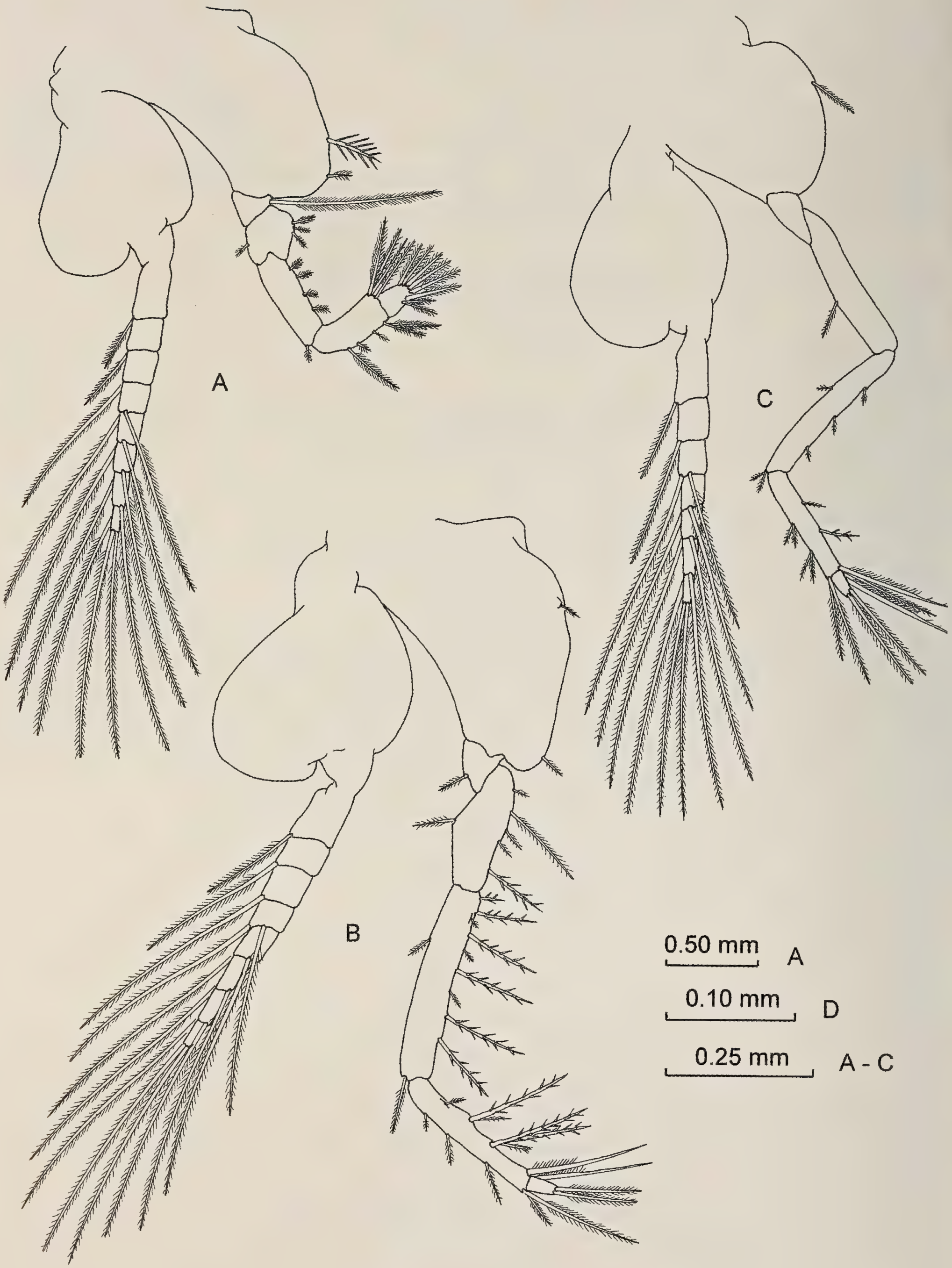

Figure 6
Anisomysis comorensis sp. nov.
Adult male: (A) second thoracic limb. (B) fourth thoracic limb. (C) eighth thoracic limb.

male pleopod biramous, endopod short and unsegmented (Fig. 7B); exopod three-segmented and reaching beyond base of telson. First exopod segment 4.6 and 2.1 times longer than second and third segments respectively, third segment 2.1 times longer than second, terminal setae subequal in length; form typical for the genus (Fig. 7C). Female pleopods rudimentary, becoming progressively smaller posteriorly.

Uropods long and narrow, setose all round; exopod distinctly longer than endopod and curved slightly outward (Fig. 7D). Exopod of uropod nearly three times length of telson. Telson (Fig. 7E) 1.6 times longer than basal width, proximal half with convex margins and unarmed, distal half concave and gradually narrowing towards truncated apex. Distal width less than one-third as broad as maximum basal width. Distal margin with minute notch in some specimens, three unequal spines on either side. Lateral margins with 10–13 spines.

Length: adult male 4.5–5.2 mm; adult female 3.8–4.6 mm.

Etymology

The specific name refers to the region from where collections were made.

Remarks

In the absence of denticles on the second segment of the mandibular palp and in the telson having a truncated apex, *Anisomysis comorensis* sp. nov. displays affinities to *A. hanseni* Nouvel, 1967, *A. levi* Băcescu, 1973*b*, *A. vasseuri* Ledoyer, 1974, *A. bacescui* Pillai, 1976, *A. chessi* Murano, 1983 and *A. mullini* Murano, 1987. Among these, *A. comorensis* sp. nov. shows closest resemblance to *A. bacescui* in the shape and armature of the telson. It differs from *A. bacescui* in the following points:

1. The carpopropodus of the thoracic endopods three to eight in *A. bacescui* is unsegmented. It is two-segmented in *A. comorensis* sp. nov.
2. The lateral border of the telson in *A. bacescui* has 10–13 spines along the border as opposed to 9 in the new species.
3. In the former species, the fourth pleopod of the male extends slightly beyond the base of the telson, whereas in *A. comorensis* sp. nov. it extends to the tip of the telson.
4. Body size is larger in the new species, measuring up to 5.2 mm compared to 2.7 mm in *A. bacescui.*

The new species also closely resembles *A. hanseni*, but the latter has a distinct telsonic sinus.

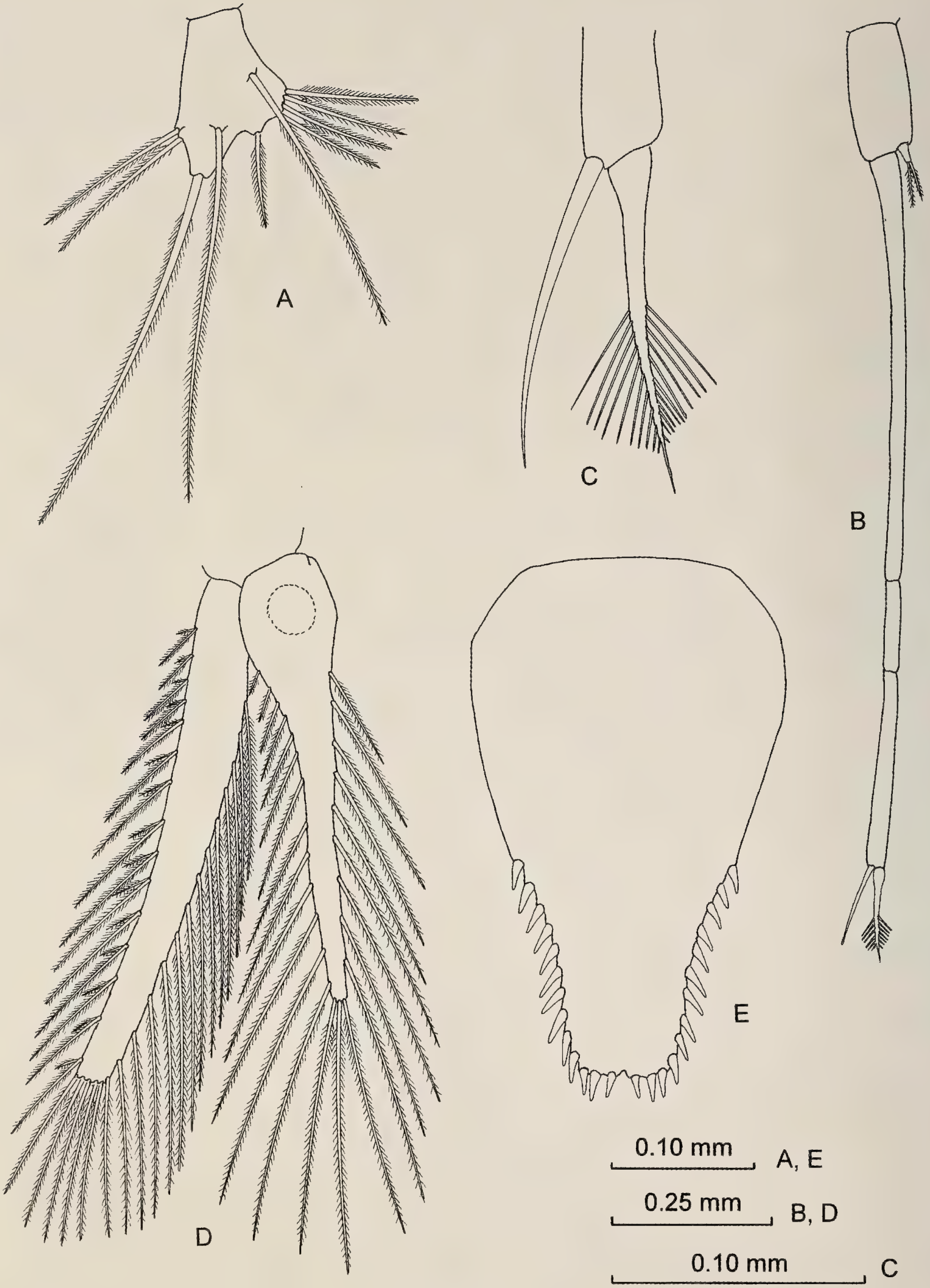

Figure 7
Anisomysis comorensis sp. nov.
Adult male: (A) first pleopod. (B) fourth pleopod. (C) distal end of exopod of fourth pleopod. (D) uropod. (E) telson.

TABLE 1

Distribution of *Anisomysis* species recorded from the Western Indian Ocean Region.

Species	Distribution
A. arabicus Wooldridge & Victor, 2004	Oman (Wooldridge & Victor 2004)
A. bacescui Pillai, 1976	Lakshadweep archipelago (Panampunnayil 1993), Arabian sea (Müller 1993)
A. bifurcata Tattersall, 1912	Chagos and Farquehan Islands (Tattersall 1912)
A. comorensis sp. nov.	Grande Comore (this publication)
A. hanseni Nouvel, 1967	Madagascar (Nouvel 1967), Grande Comore (this publication), Tanzania (Băcescu 1975)
A. ijimai estafricana Băcescu, 1973*c*	Kenya (Băcescu 1973*c*)
A. kunduchiana Băcescu, 1975	Tanzania (Băcescu 1975)
A. laccadivei Panampunnayil, 1981	Lakshadweep archipelago (Panampunnayil 1981)
A. levi Băcescu, 1973*b*	Red Sea (Băcescu 1973*b*)
A. marisrubri Băcescu, 1973*a*	Mozambique (Wooldridge & Mees 2003), Tanzania (Băcescu 1975), Kenya (this publication), Red Sea, (Băcescu 1973*a*, Almeida Prado-Por 1980), Grande Comore (this publication)
A. sirielloides Băcescu, 1975	Tanzania (Băcescu 1975)
A. spinata Panampunnayil, 1993	Lakshadweep archipelago (Panampunnayil 1993)
A. truncata Panampunnayil, 1993	Lakshadweep archipelago (Panampunnayil 1993)
A. unispinosa sp. nov.	Grande Comore (this publication)
A. vasseuri Ledoyer, 1974	Madagascar (Ledoyer 1974)

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SYSTEMATIC papers must conform to the International code of zoological nomenclature (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc. The name of the taxon should be followed, without intervening punctuation, by the author's(s') name(s) (not abbreviated) and the year of publication; a comma must separate author's(s') name(s) and year. The author's(s') name(s) and date must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be either according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order (see example 1), or according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry (see example 2). The author should adopt one style or the other throughout a paper.

Family **Nuculanidae**
Nuculana (Lembulus) bicuspidata (Gould, 1845)
Figs 14–15A

Example 1

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata (Gould) Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871, pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata (Gould): Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

NOTE punctuation in the above example: comma separates author's name and year; semicolon separates more than one reference by the same author; full stop separates references by different authors; figures of plates are enclosed in parentheses to distinguish them from text-figures; dash, not comma, separates consecutive numbers.

Example 2

1845 *Nucula (Leda) bicuspidata* Gould, p. 37.
1856 *Leda plicifera* A. Adams, p. 50.
1859 *Laeda bicuspidata* (Gould) Hanley, p. 118, pl. 228 (fig. 73).
1861 *Nucula largillierti* Philippi, p. 87.
1871 *Laeda bicuspidata* (Gould): Sowerby, pl. 2 (fig. 8a–b).
1950 *Leda bicuspidata* (Gould): Nicklès, p. 163, fig. 301.
1955 *Leda bicuspidata* (Gould): Nicklès, p. 110.
1964 *Leda bicuspidata* (Gould): Barnard, p. 234, figs 8–9.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated allotype (if applicable) and/or paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype. SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33 51 S 25 39 E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text, e.g. '... the Figure depicting *C. namacolus* ...', or '... in *C. namacolus* (Fig. 10) ....'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names: e.g. Du Toit, but A. L. du Toit; Von Huene, but F. von Huene

(c) Scientific names, but not their vernacular derivatives e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary. Reference to the author should preferably be expressed in the third person. **Roman numerals** should be converted to arabic, except when forming part of the title of a book or article, e.g. 'Revision of the Crustacea. Part VIII. Amphipoda.'. A **specific name** must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter (except at the beginning of a sentence or paragraph), provided the same generic name is used consecutively. The name of **new genus or species** should not be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of *Biological Abstracts*.

GENERAL. Once referees' reports have been received by the editor, these will be discussed by the editorial committee. If the paper is considered acceptable after minor or major revision, the reports will be forwarded to the author who must then thoroughly revise in accordance with the referees' suggestions. Final acceptance of the revised manuscript will be considered by the editorial committee. In the case of major revision being necessary, the committee reserves the right to consult one or more referees regarding the revised manuscript.

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